Distribution and Feeding Responses of Juvenile Chum Salmon *(Oncorhynchus keta)* to Thermal Change in Seawater

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DISTRIBUTION AND FEEDING RESPONSES OF JUVENILE CHUM SALMON (*ONCORHYNCHUS KETA*) TO THERMAL CHANGE IN SEAWATER

by

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PREFACE

This report is one in a series that describe the results of field and laboratory studies on the effect of heated seawater on juvenile chum salmon (*Oncorhynchus keta*). The studies were initiated in response to potential increases in the thermal discharge from British Columbia Hydro and Power Authority's (B.C. Hydro) Burrard Generating Station, into the marine waters of Port Moody Arm, Burrard Inlet, B.C. This gas-fired steam electric station operates under a permit from the provincial government, and utilizes a once-through seawater cooling system. The permit allows for the discharge of up to 1.7 million m^3 daily of heated cooling waters ($\leq$ 27 °C), drawn from, and discharged to, Port Moody Arm. An environmental impact study to assess any effects due to the thermal discharge was a requirement of an amendment to the provincial permit. An environmental assessment study plan was submitted by B.C. Hydro to federal and provincial regulatory authorities in 1996, and it was approved in 1997.

The Department of Fisheries and Oceans entered into a co-operative research venture with B.C. Hydro on selected aspects of the environmental assessment. Other studies investigated the effects of the thermal effluent on the growth of juvenile chum salmon, the heat budget of Port Moody Arm and the input from mud flats, an assessment of the potential effects of the effluent on migrating and resident fish, and the potential effects on planktonic organisms drawn into the plant and those entrained in the thermal effluent plume. Reports on these studies were provided to B.C. Hydro in December 1997 and those undertaken by the Department of Fisheries and Oceans are also to be published in the scientific literature.

The Department of Fisheries and Oceans undertook two studies in 1997:

1) The behavior of chum salmon in response to heated seawater was investigated in the laboratory using a water column simulator that mimicked conditions the fish may encounter in Port Moody Arm. Their behavior was examined under controlled conditions during a changing thermal regime and under thermally stratified conditions. The response of the fish to food, their swimming, and school positions were quantified in relation to the experimental conditions.

2) Preference-avoidance" cages (6.0 m x 0.5 m x 0.5 m) were used in Port Moody Arm to examine the vertical distribution of chum salmon at a reference location and at sites 70 m, 250 m, and 1200 m from the "cooling water" discharge source. The results were related to the ambient aquatic conditions to reveal differences or similarities in the vertical distribution of salmon with proximity to the discharge location, and to identify variables that accounted for these changes.

TABLE OF CONTENTS

ABSTRACT vii

RÉSUMÉ x

LIST OF TABLES xiii

LIST OF FIGURES xiv

INTRODUCTION 1

METHODS AND MATERIALS 4

Fish transport and maintenance 4

Water Column Simulator 5

Research design and experimental protocol 7

Feeding in a thermal gradient 8

Swim speed 8

Excursion times 8

Transition to thermal stratification 8

Digital image analysis 9

Thermal resistance bioassay 10

Apparatus 10

Protocol 10

Supplementary experiments 11

RESULTS 12

Thermal resistance bioassays 12

Water Column Simulator studies 12

TABLE OF CONTENTS (cont'd.)

Influence of temperature rise and the presence of food in the surface waters of the WCS 13

Location of individual chum salmon and the school under isothermal and thermally-stratified conditions with and without the presence of food 18

Acute response to elevated TGP and feeding on live prey at 18°C, 25°C, and 30°C 19

Behavioral response of chum salmon to temperature during a change from isothermal to thermally-stratified conditions 21

Location of individual chum salmon and the school during the thermal transition period 24

DISCUSSION 24

Thermal resistance 25

Thermal resistance and TGP 26

Behavioral thermoregulation and activity in isothermal and thermally stratified seawater 28

Isothermal conditions 28

Response to thermal change and stratification 29

Thermal preference and regulatory behavior 30

Avoidance of heated seawater 31

Influence of temperature and food on the distribution, swimming, feeding and use of surface waters 32

Acute response to elevated TGP and feeding on live prey at 18 °C, 25 °C, and 30 °C 34

Swim speed 34

Use of "sub-optimal" waters 34

TABLE OF CONTENTS (cont'd.)

SUMMARY AND CONCLUSIONS 36

ACKNOWLEDGEMENTS 38

REFERENCES 39

FIGURES AND TABLES 49

ABSTRACT

Birtwell, I.K., J.S. Korstrom, R.P. Fink, J.A. Tanaka, D.I. Tiessen, and B.J. Fink. 2001. Distribution and feeding responses of juvenile chum salmon (*Oncorhynchus keta*) to thermal change in seawater. Can. Tech. Rep. Fish. Aquat. Sci. 2342: 93 p.

The response of juvenile chum salmon (*Oncorhynchus keta*) to heated seawater was studied between May and August 1997. This period coincides with their seasonal utilization of marine waters adjacent to a natural gas-fired steam-electric generating station which discharges up to 1.7 billion $L \cdot d^{-1}$ of "cooling water" (≤ 27 °C) into the marine waters of Port Moody Arm in Burrard Inlet, British Columbia.

Chum salmon exposed to heated seawater at air saturated dissolved gas levels (√ ± S.D.: 24.9 ± 0.3 °C; 100.6 ± 0.6%), and elevated total gas pressure (TGP) levels (25.0 ±0.3 °C; 109.1 ± 0.8%) died at similar rates in flow-through bioassays. The mean (and median) time to 50% mortality was 157 ± 47 min (157 min) and 159 ± 57 min (150 min), respectively. The first fish died after 50 min exposure to 25 °C water at air saturation, and at 65 min in waters with elevated TGP. The corresponding maximum survival times were 304 and 343 min. There was no discernible effect of TGP on the resistance of the chum salmon to the 25 °C waters.

The volitional responses of a school of 20 juvenile chum salmon were studied during eight 7-d experiments in a 4500 L flow-through water column simulator (WCS). The experimental conditions were chosen to mimic changes that could occur during the commencement of thermal discharge from the intermittently operating electric generating plant. The activity and school location of chum salmon were examined under isothermal and vertically stratified seawater conditions. The effect of food on fish location and activity was examined under stable isothermal and stratified regimes.

Under isothermal condition (10 °C), the schooled fish were biased towards the water surface (median position <1 m). Significant increases in school volume, number of fish in surface waters (√ 27.4 to 62.0 %), and swim speed (√ 4.0 $cm \cdot s^{-1}$ to 9.4 $cm \cdot s^{-1}$) occurred when the fish were feeding on food presented from the surface.

During the transition to thermally stratified conditions, the school moved to occupy surface waters which were warmer than acclimation temperatures, and thereafter moved downwards in the water column as the temperature of the water above the thermocline increased to a mean value of 24.0 ± 1.4 °C.

A tri-phase model (based on a piece-wise non-linear regression) was used to describe the distribution shifts of chum salmon over 4 h during a change from isothermal (10 °C) to thermally stratified conditions. The temperature of the water above the thermocline at which 50% of fish chose to move into warmer waters was 12.2 °C, and that at which 50% moved downwards and avoided increasing surface water temperatures was 20.2 °C. The model permitted the

determination of a maximum response, more accurately defining the preferred temperature of >83.5% of the fish to be between 13.7 °C and 17.9 °C. In the thermally stratified water column, the majority of fish occupied a position in the thermocline rather than returning to deeper and cooler waters. The occupation of the thermocline by 50% of the fish occurred at 21.3 °C. Despite the potentially lethal temperatures in overlying surface waters, chum salmon continued to enter these waters, albeit for shorter periods than under isothermal conditions (√ 3.2 s vs >23.3 s).

The number of fish that occupied the waters above the thermocline during conditions of thermal stratification and those occupying the same layer under isothermal conditions were compared, with and without the presence of food presented from the water surface. Temperature and food caused a significant difference in the number of fish in the surface waters and at the thermocline, but not in the sub-thermocline waters.

Under isothermal conditions the presence of food resulted in a significant increase in the number of fish entering surface waters to feed (√ 27.4% to 62.0%), distribution shifts of the school, and significantly increased swim speed (√ 4.0 $cm \cdot s^{-1}$ to 9.4 $cm \cdot s^{-1}$), but did not influence the duration of time spent in these waters.

When the temperature of waters above the thermocline was at potentially lethal levels (24°C), marked avoidance of these waters occurred. Significantly fewer fish (√ 2.2% vs 27.4%) used the warmer waters for significantly shorter periods of time (√ 3.2 s vs >23 s). Under these conditions swim speeds remained similar to those recorded under the cooler isothermal conditions.

Relative to thermally stratified conditions without food present, the provision of food in surface waters above the thermocline resulted in a movement of fish (√ 2.2% to 29.8 %) to feed in the warmer waters. At the same time, duration of the excursions was significantly elevated (√ 3.2 s to 10.7 s) as was the swim speed (√ 4.0 $cm \cdot s^{-1}$ to 17.3 $cm \cdot s^{-1}$). Thus the chum salmon spent more time in the potentially lethal high temperature waters when feeding, and the obviously protective and adaptive avoidance responses were temporarily overridden by the presence of food and the motivation to feed. Comparing the response of the salmon to the presence of food under isothermal and thermally-stratified conditions, the latter conditions resulted in fewer fish (√ 29.8 % vs 62.0 %) in the surface waters, but they swam significantly faster (√ 17.3 $cm \cdot s^{-1}$ vs 9.4 $cm \cdot s^{-1}$) and made briefer excursions (√ 10.7 s vs >23.3 s).

Juvenile chum salmon fed on live prey (*Artemia* sp.) in potentially lethal waters at 25 °C and at 30 °C, with and without elevated TGP.

These experiments demonstrated that underyearling chum salmon of differing age and size (weight √ 1.4 ± 0.4 to 15.9 ± 3.8 g; length √ 56.3 ± 4.3 to 117.0 ± 9.0 mm) reacted similarly to thermal changes in seawater. Although they may avoid habitats in which temperatures exceed preferred levels, they will rapidly utilize these "sub-optimal" waters for feeding, even entering waters at temperatures that are potentially acutely lethal to them. Any cumulative effects of such transient excursions on the wellbeing of chum salmon are unknown.

Key words: *Oncorhynchus keta*, seawater, temperature, behavior, distribution, thermal preference, avoidance, swim speed, feeding.

RÉSUMÉ

Birtwell, I.K., J.S. Korstrom, R.P. Fink, J.A. Tanaka, D.I. Tiessen, and B.J. Fink. 2001. Distribution and feeding responses of juvenile chum salmon (*Oncorhynchus keta*) to thermal change in seawater. Can. Tech. Rep. Fish. Aquat. Sci. 2342: 93 p.

La réaction des saumons kétas juvéniles (*Oncorhynchus keta*) en réponse à une eau de mer chauffée a été étudiée de mai à août 1997. Cette période coïncide avec la saison pendant laquelle ces poissons fréquentent les eaux marines au voisinage d'une centrale thermique alimentée au gaz naturel qui décharge jusqu'à 1.7 milliard $L \cdot d^{-1}$ d'eau de refroidissement (≤ 27°C) dans les eaux du bras Port Moody, bras Burrard, Colombie-Britannique.

Les saumons kétas exposés à une eau de mer chauffée caractérisée par des teneurs en gaz dissous correspondant à une saturation en air (√ ± É.-T. : 24.9 ± 0.3 °C; 100.6 ± 0.6 %) ou par une pression totale des gaz [PTG] élevée (25.0±0.3°C; 109.1±0.8%) mouraient à une fréquence similaire dans les bioessais à circulation continue. Les intervalles moyens (et médians) avant la mort de 50 % des poissons étaient de 157 ± 47min (157min) et de 159 ± 57min (150min), respectivement. Le premier poisson est mort après une exposition de 50 minutes à une eau à 25 C saturée en air dissous, et de 65 minutes à une eau ayant une PTG élevée. Les temps de survie maximaux étaient de 304 et de 343 minutes, respectivement. On n'a relevé aucun effet décelable de la PTG sur la résistance des saumons kétas dans des eaux à 25°C.

Les réactions volontaires d'un banc de 20 saumons kétas juvéniles ont été étudiées au cours d'expériences de 7 jours dans un simulateur à colonne d'eau à circulation continue. Les conditions expérimentales ont été choisies de manière à reproduire fidèlement les changements se produisant au début d'une décharge thermique par la centrale fonctionnant de manière intermittente. L'activité et la localisation du banc de saumons kétas ont été examinées en isothermie et en stratification verticale. L'effet de la présence de nourriture sur la localisation et l'activité des poissons a été examiné en conditions stables d'isothermie et de stratification.

En conditions d'isothermie (10°C), les poissons en banc manifestaient une préférence envers les eaux de surface (position médiane <1m). Une augmentation significative du volume du banc, du nombre de poissons dans les eaux de surface (√ 27.4% à 62.0%) et de la vitesse de nage (√ 4,0 $cm \cdot s^{-1}$ à 9,4 $cm \cdot s^{-1}$) a été observée lorsque les poissons se sont alimentés avec de la nourriture présentée par la surface.

Au cours de la transition vers les conditions de stratification thermique, le banc s'est déplacé pour s'établir dans les eaux de surface, dont la température était supérieure aux températures d'acclimatement, puis est descendu dans la colonne d'eau à mesure que la température de l'eau au-dessus de la thermocline augmentait jusqu'à une valeur moyenne de 24.0 ± 1.4°C.

Les variations de distribution des saumons kétas sur un intervalle de 4 heures lors du passage de l'isothermie (10°C) à des conditions de stratification thermique ont été étudiées au moyen d'un modèle triphasique (basé sur une régression non linéaire pas-à-pas). La température de l'eau au-

dessus de la thermocline à laquelle 50% des poissons sont retournés à des eaux plus chaudes était de 12.2 C, et la température à laquelle 50% des poissons se sont déplacés vers le bas pour éviter le réchauffement de surface était de 20.2°C. Ce modèle a permis de déterminer une réponse maximale et de définir plus précisément que la température préférée de >83.5% des poissons se situait entre 13.7°C et 17.9°C. Dans la colonne d'eau stratifiée selon la température, la plupart des poissons sont restés dans la thermocline plutôt que de retourner dans les eaux plus profondes et plus froides. C'est à 21.3 C que 50% des poissons occupaient la thermocline. Malgré les températures potentiellement létales des eaux de surface, les saumons kétas ont continué de fréquenter ces eaux, bien que pour des périodes plus courtes qu'en isothermie (√ 3.2s contre >23.3s).

Le nombre de poissons qui occupaient les eaux au-dessus de la thermocline pendant la stratification thermique et ceux qui occupaient la même couche en isothermie ont été comparés, avec et sans la présence de nourriture présentée depuis la surface. La température et la nourriture ont provoqué une différence significative ($p \leq 0.05$) dans le nombre de poissons fréquentant les eaux de surface et la thermocline, mais pas les eaux inférieures à la thermocline.

En isothermie, la présence de nourriture a entraîné une augmentation significative du nombre de poissons entrant dans les eaux de surface pour se nourrir (√ 27.4% à 62.0%), un déplacement de la distribution du banc et une augmentation significative de la vitesse de nage (√ 4.0cm·s^{-1} à 9.4cm·s^{-1}), mais sans modifier le temps passé par les poissons dans ces eaux.

Un évitement marqué des eaux au-dessus de la thermocline a été observé aux températures potentiellement létales (24 °C). Un nombre significativement moins élevé de poissons (√ 2.2% contre 27.4%) fréquentait les eaux plus chaudes pendant des périodes significativement plus courtes (√ 3.2s contre >23s). Dans ces conditions, les vitesses de nage sont restées comparables à celles qui ont été enregistrées en conditions isothermes, plus froides.

Comparativement aux conditions de stratification thermique en absence de nourriture, l'apport de nourriture dans les eaux de surface au-dessus de la thermocline a suscité un déplacement des poissons (√ 2.2% à 29.8%) en direction des eaux plus chaudes. En même temps, la durée des excursions était significativement augmentée (√ 3.2s à 10.7s), de même que la vitesse de nage (√ 4.0cm·s^{-1} à 17.3cm·s^{-1}). Pendant qu'ils se nourrissaient, les saumons kétas ont ainsi passé plus de temps dans les eaux plus chaudes, à une température potentiellement létale, alors que les réactions de protection et les réactions adaptatives d'évitement ont été temporairement inhibées par la présence de nourriture et la motivation nutritionnelle. Lorsque l'on compare les réactions induites par la présence de nourriture en isothermie et en stratification thermique, la stratification thermique a entraîné une diminution du nombre de poissons dans les eaux de surface (√ 29.8% contre 62%), mais une augmentation significative de la vitesse de nage (√ 17.3cm·s^{-1} contre 9.4cm·s^{-1}) et un raccourcissement des incursions (√ 10.7s contre >23.4s).

Les saumons kétas juvéniles se nourrissaient de proies vivantes (*Artemia* sp.) dans les eaux atteignant une température potentiellement létale de 25 C et de 30 C, avec ou sans élévation de la PTG.

Ces expériences ont démontré que les jeunes saumons kétas de moins d'un an (âge et taille variables; √ poids : 1.4 ± 0.4 à 15.9 ± 3.8g; √ longueur : 56.3 ± 4.3 à 117.0 ± 9.0mm) réagissent de manière comparable aux modifications thermiques de l'eau de mer. Bien qu'ils évitent normalement les habitats où la température excède leurs températures préférées, ils n'hésitent pas à fréquenter ces eaux «suboptimales» pour se nourrir, s'aventurant même dans des eaux dont la température leur est potentiellement létale. On ignore toutefois quels sont les éventuels effets cumulatifs de ce genre d'incursions transitoires sur la santé des saumons kétas.

Mots clés : *Oncorhynchus keta*, eau de mer, température, comportement, distribution, préférences thermiques, évitement, vitesse de nage, nourriture.

LIST OF TABLES

Table 1. Schedule of nine 50 min observation periods during each five day experiment..49

Table 2. Summary of time to death data for juvenile chum salmon exposed to heated seawater at air saturation and supersaturation 50

Table 3. Determinations of temperature (mean ± S.D.) during the transition to thermally stratified conditions in the WCS aquarium during experiments 1 – 8 51

Table 4. Percentage of fish in the three zones of the WCS aquarium over 8 experiments, by observation period 53

Table 5. Results of statistical comparisons (t-tests) of the percentage of chum salmon in 3 vertical zones of the WCS aquarium under 6 experimental conditions (n = 8) 54

Table 6. Results of statistical comparisons (t-tests) of the swim speed (n = 147 – 167) of juvenile chum salmon under 6 experimental conditions (n = 8) in the WCS aquarium. 55

Table 7. Results of statistical comparisons (t-tests) of the time chum salmon spent in the top zone of the WCS aquarium under 5 experimental conditions (n = 8). 56

Table 8. Distribution of chum salmon in relation to different thermal regimes (18, 25, 30°C), total gas pressure, and the presence of food in the WCS aquarium (n = 1) 57

Table 9. The results of piece-wise non-linear regression analysis applied to the percentage of fish in the top zone of the WCS aquarium over 7 experiments 58

Table 10. Robustness test results of the piece-wise non-linear model run with (n-1) weeks to determine if the estimates of k1 and k2 changed with data removal. 59

LIST OF FIGURES

Figure 1. Water Column Simulator schematic 60

Figure 2. Time mortality curves for juvenile chum salmon exposed to 25° C seawater (± elevated TGP) 61

Figure 3. Temperature changes recorded by data loggers (#1-#12) at specific depths in the WCS aquarium during transition from isothermal to thermally stratified conditions 62

Figure 4. Precise location of individual chum salmon in the WCS aquarium (observation period 1 - isothermal AM) 63

Figure 5. Precise location of individual chum salmon in the WCS aquarium (observation period 3 - isothermal AM) 63

Figure 6. Precise location of individual chum salmon in the WCS aquarium (observation period 5 - isothermal AM) 64

Figure 7. Precise location of individual chum salmon in the WCS aquarium (observation period 9 - isothermal AM) 64

Figure 8. Precise location of individual chum salmon in the WCS aquarium (observation period 7 - thermally stratified AM) 65

Figure 9. Precise location of individual chum salmon in the WCS aquarium (observation period 2 - isothermal PM) 65

Figure 10. Precise location of individual chum salmon in the WCS aquarium (observation period 4 - isothermal, food PM) 66

Figure 11. Precise location of individual chum salmon in the WCS aquarium (observation period 6 - thermally stratified PM) 66

Figure 12. Precise location of individual chum salmon in the WCS aquarium (observation period 8 - thermally stratified, food PM) 67

Figure 13. Response of juvenile chum salmon to temperature change in the surface waters of the WCS aquarium, estimated by piece-wise non-linear regression 68

LIST OF FIGURES (cont'd.)

Figure 14. Presence of juvenile chum salmon in the thermocline during temperature change in the surface waters of the WCS aquarium, estimated by piece-wise non-linear regression 69

Figure 15. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 10.4 - 11.3°C 70

Figure 16. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 11.3 - 12.1°C 70

Figure 17. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 12.1 - 13.1°C 71

Figure 18. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 13.1 - 14.1°C 71

Figure 19. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 14.1 - 15.2°C 72

Figure 20. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 15.2 - 16.0°C 72

Figure 21. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 16.0 - 17.1°C 73

Figure 22. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 17.0 - 18.0°C 73

Figure 23. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 18.0 - 19.0°C 74

Figure 24. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 19.0 - 20.0°C 74

Figure 25. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 20.0 - 21.1°C 75

Figure 26. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 21.1 - 22.0°C 75

Figure 27. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 22.0 - 23.0°C 76

LIST OF FIGURES (cont'd.)

Figure 28. Precise location of individual chum salmon in the WCS aquarium - top zone temperature 23.0 - 23.7°C.....76

INTRODUCTION

The responses of fish to temperature has been studied extensively due to its' fundamental importance in the life of poikilothermic aquatic organisms as a controlling, limiting, and directive factor (Fry 1947; Brett 1952; Coutant 1977a; Reynolds 1977; Olla et al. 1980; Houston 1982; Coutant 1987; Langford 1990). Particular attention has been focused on the significance of temperature changes due to thermal discharges from nuclear and electric generating stations into fresh and marine waters (Neill and Magnuson 1974; Coutant 1975, 1977a; International Atomic Energy Agency 1975; Spigarelli 1975; Spigarelli et al. 1982; Langford 1990).

The purpose of this study is to provide additional information on the effects of temperature change on juvenile chum salmon (*Oncorhynchus keta*) in relation to potential impacts from a natural gas-fired steam-electric generating station which discharges ≤ 27°C cooling water at a maximum daily rate of 1.7×10^9 L into the marine waters of Port Moody Arm, Burrard Inlet, British Columbia. The Port Moody Arm is 6.5 km long and has an average depth of 8.8 m at low tide (Waldichuk 1965).

Chum salmon were chosen as the test species due to their abundance and prevalence (March to August) in the contiguous waters of Burrard Inlet (Nelles 1978; Macdonald and Chang 1993). In 1997, a total of 528,000 juvenile salmon were released from hatcheries into the waters of Port Moody Arm and Indian Arm, in Burrard Inlet (Korstrom et al. 1998). These releases comprised 66,000 coho salmon (*Oncorhynchus kisutch*), 184,000 chinook salmon (*Oncorhynchus tshawytscha*), and 278,000 chum salmon (M. Johnson, Department of Fisheries and Oceans, Vancouver, B.C., unpublished information). Spawning populations occur in local streams and rivers, and juveniles from these fish will also utilize the waters of Port Moody Arm and may encounter the thermal plume associated with the heated cooling water discharged by the Burrard Generating Station (BGS) into this water body.

The effects of temperature on the survival and metabolism of chum salmon have been studied primarily under freshwater conditions. Brett's (1952) comprehensive examination of the effects of temperature on the survival, resistance and tolerance of juvenile salmon (including chum salmon) remains the foremost classic work on these topics. In later years his continued research into the effects of temperature on juvenile salmon provided additional knowledge, especially relating to metabolic processes and performance (for example, Brett 1964, 1970, 1971). Brett's (1952) work revealed that the ultimate upper lethal temperature for chum salmon in fresh water was 23.8 °C, that their preferred temperature was between 12 °C and 14 °C, and that optimal growth in fresh water occurred at around 15 °C (Brett 1995). Behavioral thermoregulation, and volitional activities, especially in seawater, received little attention. More recently, laboratory and field studies have provided additional information on the response of chum salmon to temperature (Mason 1974; Manzer 1964), food (Mason 1974), and industrial effluents (Birtwell and Harbo 1980; McGreer and Vigers 1983; Birtwell and Kruzynski 1989), thereby emphasizing not only the importance of including behavioral research in environmental assessments (Coutant 1975, 1977a; Olla et al. 1980; Gray 1983, 1990; Coutant 1987) but also its potential value in the

interpretation of physiological and ecological effects (Magnuson et al. 1979; Giattina and Garton 1982; Coutant 1987).

Research on other salmonids has expanded our knowledge of the lethal (e.g. Brett 1952; Becker and Genoway 1979; Konecki et al. 1995) and sublethal (e.g. Donaldson and Foster 1941; Brett 1956, 1971; Shreck 1990) effects of elevated temperature, and the consequences on survival (Baker et al. 1995). For instance, exposure to elevated temperature has been shown, in general, to increase susceptibility to disease (Holt et al. 1975; Groberg et al. 1983; Wertheimer and Martin 1986) and predation (Sylvester 1972; Coutant 1973; Vigg and Burley 1991). There are also reports that thermal shock does not result in increased susceptibility to disease and in some tests the fish were less susceptible than controls (Poston et al. 1985). Studies by Konecki et al. (1995) have shown that thermal tolerance levels for coho salmon captured from the wild were related to their previous acclimation history (fish from cooler streams had lower thermal tolerance) and exceeded those determined under stable laboratory acclimation conditions (e.g. Brett 1952). McGeer et al. (1991) assessed the tolerance of 6 stocks of coho salmon to temperature and concluded that there was no significant difference among them. This result was attributed to their relatively similar life history patterns and geographical (latitudinal) proximity. However, the thermal tolerance of northern stocks of chinook salmon was lower than that of southern stocks with different life history patterns (Beacham and Withler 1991). The results of Konecki et al. (1995) and Beacham and Withler (1991) relate to genetic and phenotypic adaptation and expand our knowledge on the potential lethal effects of temperature under natural conditions. Short-term (hours to days) acclimation of salmon to increasing temperature occurs (Brett 1956; Coutant 1975, 1977a) but the process is limited with proximity to lethal conditions (Brett 1952). Furthermore, when presented with choices, volitional movements favor the occupation of temperatures in the preferred range (Neill and Magnuson 1974; Engel and Magnuson 1976; Levy et al. 1980; Gray et al. 1977), or those that may be more variable yet favor optimal growth and metabolism. For example, the diurnal vertical and coincident temperature shifts of rearing sockeye salmon juveniles (*Oncorhynchus nerka*) in lakes (Brett 1971; Clark and Levy 1988; Levy et al. 1990), and the enhanced growth rate of brown trout (*Salmo trutta*) (Spigarelli et al. 1982), and sockeye salmon (Biette and Geen 1980) under varying versus stable temperature regimes.

Research on the effects of temperature, in concert with other environmental stressors, has shown how some salmonid behavioral traits that are presumably adaptive may jeopardize health and survival in environments that are impacted directly or indirectly by anthropogenic activities (Coutant 1987; Birtwell and Kruzynski 1989; Birtwell et al. 1997; Korstrom et al. 1997; Jain et al. 1998). During unusually warm and stable climatic conditions, the fidelity of adult sockeye salmon to favor temperatures around 12 °C at the head of Alberni Inlet, BC, resulted in the loss of approximately 230,000 adults. The fish congregated in low dissolved oxygen waters at ~ 12°C rather than migrating into either the warm fresh waters of the Somass River, or the more oxygenated yet warmer surface estuarine waters in the Inlet. These fish became heavily parasitized with sea lice (*Lepeoptheirus salmonis)*, and migratory performance and spawning were compromised (Birtwell et al. 1997). This seemingly maladaptive behavioral trait was later confirmed, and the effects on swim performance assessed, in laboratory studies (Birtwell et al. 1994; Korstrom et al. 1996, 1997; Birtwell et al. 1997; Jain et al. 1998).

Similar use of "sub-optimal" (i.e. stressful to lethal) habitats by salmonids has been demonstrated in the field, adjacent to the discharge of pulp mill effluent (Birtwell 1977, 1978; Birtwell and Harbo 1980; Birtwell and Kruzynski 1989). Although juvenile salmon avoided concentrations of pulp mill effluent in surface waters over 3 h, they did not do so over 24 h and this resulted in the death of some individuals (Birtwell and Kruzynski 1989). The innate requirement of juvenile salmonids to occupy the uppermost surface waters during their early estuarine and sea life (Piercey et al. 1985; Macdonald et al. 1987) compromised their survival in vertically stratified waters containing pulp mill effluent (Birtwell and Kruzynski 1989). Our recent studies with chinook salmon have shown that individuals are susceptible to exposure to elevated concentrations of pulp mill effluent (>20°C) discharged to the upper Fraser River (<1 °C) under winter conditions. At this time, the fish become nocturnal and occupy intercobble substrate close to shore (and also within the effluent plume) during daylight (Emmett et al. 1996). These behavioral traits may jeopardize survival through increased exposure to elevated concentrations of pulp mill effluent, which in turn could result in a greater susceptibility to predation (Campbell et al. 1995). Similar findings have been reported for non-salmonids, revealing the potential for waters of "sub-optimal" quality to be occupied because of, for example, the choice of fish to occupy waters of a particular thermal range that facilitate their metabolic and physiological functions (thermoregulatory behavior). Marcello and Fairbanks (1974) reported that Atlantic menhaden (*Brevoortia tyranus*) were attracted to the thermally heated waters discharged from a nuclear power plant and that they died from exposure to elevated levels of total gas pressure (TGP). Although fish may avoid gas supersaturation, other factors may alter their response. Meldrim et al. (1973) noted that the golden shiner usually avoided gas supersaturation of 110% but when temperature increases of 5°C - 10°C were associated with the supersaturation, thermal preference overrode the avoidance response.

Given the complex behavioral responses of salmon and other fish species to "sub-optimal" habitats, including those that are thermally stratified, federal and provincial government regulatory authorities considered it important to examine this topic in relation to the thermal discharge from the BGS into Port Moody Arm. B.C. Hydro submitted a plan to these authorities in December 1996 that identified a number of studies to be initiated in 1997, as part of a 2-year environmental assessment (B.C. Hydro Study Plan, unpublished document, B C Hydro, Vancouver, B.C.). A research program was designed to elucidate the responses of juvenile chum salmon to thermal changes in the laboratory and the field as part of that environmental assessment. This was undertaken because of the scarcity of specific information on the behavior of chum salmon in relation to such changes, and the documented potential for juvenile salmon to occupy waters of "sub-optimal" quality. We speculated that the fish would tend to occupy surface waters in the marine environment of Burrard Inlet, as documented in other locations (Birtwell and Harbo 1980), and that their dispersion in the water column would be related to the prevailing conditions. Because of the variable nature of the waters around the thermal discharge from the electric generating station, and the tendency of the heated water to occupy surface waters (Seaconsult Marine Research Ltd. 1995), we employed an experimental cage technique (Birtwell 1977; McGreer and Vigers 1983). Each rectangular cage was 6m in length 0.5 m deep and 0.5 m wide. The cages were partitioned into six 1m compartments interconnected by gates that provided separation of, or access to, the enclosed water column. By placing juvenile chum

salmon into each compartment of the apparatus and permitting them access to the enclosed 6 m water column for approximately 1 d before closing the gates, we were able to determine their vertical distribution within the waters of Port Moody Arm. The cages were deployed at a reference location and at 3 other sites 70 m, 250 m, and 1200 m, from the thermal discharge from the BGS during June, July, and August 1997. The results of these studies are reported by Birtwell et al. (1998).

As part of the research studies reported here, a Water Column Simulator (WCS; Birtwell and Kruzynski 1987), was employed to study aspects of the behavior of juvenile chum salmon in the laboratory, under controlled conditions. Experimental conditions were chosen to mimic their entry to marine waters and their potential encounter with the thermal plume in Port Moody Arm created by the heated cooling water discharged from the BGS. Seawater used in these experiments was drawn from the contiguous waters of English Bay. A series of acute lethal toxicity tests with juvenile chum salmon in seawater was undertaken as part of these controlled behavioral studies to determine the ability of the fish to survive short-term (few hours) exposure to a single high temperature (~25 °C) with or without TGP supersaturation. The results of these bioassays were used to assist in the interpretation of the findings of fish behavior within the WCS in response to thermal change.

We anticipated that the chum salmon would avoid heated water, but that this avoidance could be mediated through the presence of food and the motivation to feed. Accordingly, we examined the behavior and distribution of a population of juvenile chum salmon with and without the presence of food under isothermal (acclimation) conditions followed by a transition to stable, vertically-stratified conditions in which heated water (24 °C) was separated from cooler waters at the 10 °C acclimation temperature, by a narrow thermocline. The volitional position of fish in the water column was determined together with swim speed, and duration of time spent in heated surface waters relative to baseline isothermal conditions in a 9-factor experimental design. The complete set of experimental data pertaining to these experiments is presented in the report by Korstrom et al. (1998).

MATERIALS AND METHODS

FISH TRANSPORT AND MAINTENANCE

On May 9, 1997, 2000 juvenile chum salmon (fork length 38.6 ± 2.1 mm (mean ± S.D.), weight 0.41 ± 0.09 g), were transported from fresh water within the Seymour River Volunteer Hatchery in North Vancouver, B.C. to seawater holding facilities at the West Vancouver Laboratory. The transport of fish from the hatchery occurred when fry would be entering salt water in the wild. Typically, chum salmon fry emerge from the gravel and promptly migrate downstream to estuarine waters at a size of 30-40 mm (Healey 1982; Salo 1991). Transport was accomplished within 2 h using a truck fitted with a 500-L insulated plastic tank supplied with compressed air from a portable compressor unit. A mesh bag containing 500 g Ammonex (Argent Chemical Laboratories, Redmond, WA), natural clay that rapidly binds to, and eliminates

ammonia, was placed in the transport tank. To reduce osmotic stress during the rapid transition to seawater from the fresh water hatchery environment the transport tank also contained an approximately isosmotic saline solution (10 ‰) at 7.5 °C.

At the laboratory, the fish were vaccinated against *Vibrio sp.* using an immersion bath technique with BIOVAX 1300 (Alpharma, Bellevue, WA), a prophylactic health management tool. *Vibrio sp.* are opportunistic bacterial pathogens of fish which are ubiquitous in marine and estuarine environments. BIOVAX 1300 is a water based, whole cell bacterin formulated from killed *Vibrio anguillarum* serotype 1 and *Vibrio ordalii* bacteria. The bacterin suspension was diluted in the transport tank water (1:100) and aerated for 1 h. Following vaccination, the fish were transferred, using a low abrasion dip net, to a 2500 L outdoor holding tank continuously supplied with air-equilibrated seawater (salinity 27 ± 1.4 ‰, temperature 11.4 ± 0.9 °C, and dissolved oxygen 96.3 ± 5.3% air saturation). Water flow was delivered to the tanks at approximately 46 $L \cdot min^{-1}$, which ensured a 90% replacement within 3 h (Sprague 1969). Fish density was maintained at ≤ 2 $kg \cdot m^{-3}$, and flow-loading density at ≤ 0.5 $kg \cdot L^{-1} \cdot min^{-1}$.

Stock fish were fed a ration of dry pellets (Moore Clarke, Vancouver, B.C.; Nutra C starter feed #1, #2, #3 and 1.5mm pellet) at 7.6% mean body $weight \cdot d^{-1}$. The ration was calculated assuming the maximum growth rate (5.7% body $weight \cdot d^{-1}$) for chum salmon under experimental conditions (LeBrasseur 1969) with an estimated conversion rate of 75%. Food delivery was via an automatic belt feeder (Zeigler Bros Ltd., Gardner, PA.) set for continuous operation from dawn to dusk to avoid habituation on a set feeding schedule, which may have biased subsequent experimental observations. The salmon were held under a natural photoperiod and were acclimated for a period of at least 3 weeks prior to experimentation. Mean mortality rate in the stock tank was negligible at 0.009% per day, well below mortality guidelines established by Sprague (1973) when accepting or rejecting a population of fish for use in aquatic toxicity tests.

WATER COLUMN SIMULATOR

Birtwell and Kruzynski (1987) have described a Water Column Simulator (WCS) which can mimic the physical vertical structure of marine waters found in coastal waters of British Columbia and therefore only a brief mention will be made of the significant components. The WCS consists of a 4500 L acrylic aquarium (2.4 m x 2.4 m x 0.8 m) with three separate water delivery loops, which facilitate the formation of a flowing, vertically stratified water column. The water column can be divided for physico-chemical monitoring into three equal zones (referred to respectively as top, middle, and bottom) each 0.74 m in depth. The system permits the controlled and varied (zone-independent) manipulation of temperature, salinity, dissolved oxygen and water velocity in each zone. Figure 1 illustrates the main components of the apparatus, as used in these experiments with heated seawater. During our experiments the waters of the WCS aquarium were either isothermal or thermally stratified with the top warmer zone overlying the deeper and cooler waters. Thus the water column was divided into 3 unequal layers during conditions of thermal stratification, namely a surface (0.74 m), a thermocline (0.09 m), and a bottom zone (1.39 m).

Continuous monitoring of incoming water parameters such as temperature (Action Instruments Company Inc., San Diego, CA., Visipak VIP501 RTD digital temperature indicator and probes; accuracy ± 0.1 °C, range 0 to 60 °C), conductivity (Rosemount Instruments Ltd., Uniloc Division, Model 112-09 sensor and Model 750C-0304 analyzer/transmitter; accuracy ± 2% full scale, range 0 to 50,00 µmhos), and dissolved oxygen (Point 4 Systems, Port Moody B.C., PT4 Oxygen Monitor; accuracy ± 2%, range 0 to 51 $mg \cdot L^{-1}$) was enabled through the use of a computerized data acquisition system (Bentek Systems Ltd., Vancouver, B.C.; Genesis Control and Monitoring Software, Iconics Inc. 1992). A significant modification to the system described by Birtwell and Kruzynski (1987) occurred for the purpose of this study resulting in an improvement in the precise control of temperature in waters entering the WCS aquarium. The incorporation of a closed-loop heat exchanger/refrigeration system, which encompasses two chillers, a compressor, condenser, water pump, and an interconnecting refrigerant piping system, modulated the temperature of incoming water. Three-way control valves mounted with self adjusting, motorized, integrated valve actuators (Honeywell Ltd., North York, ON, ML-7984) are used with electronic modulating signal controllers (Honeywell Ltd., North York, ON, T775E Remote Temperature Controller; accuracy ± 1 °C at 25 °C) to regulate the chilled water supply to three heat exchangers. Temperature controllers are connected to temperature sensors immersed in the experimental water through an aperture in the water delivery pipe 30 cm upstream of the heat exchangers. The temperature set point on the three controllers could be adjusted independently, and determined the temperature of water circulating in each zone of the WCS. Temperature was also monitored in the aquarium by twelve data loggers (Onset Stowaway Tidbit waterproof temperature logger, Onset Computer Corporation, Pocasset, MA, USA, ± 0.2 °C accuracy, -5 to 37 °C range) fastened vertically to a Velcro™ strip spanning the height of the water column. The loggers were positioned evenly in the top and bottom zones and proximal to each other over the thermocline region.

Total dissolved gas pressure (TGP) determinations were made using 3 tensionometers (Model 300C, Alpha Designs Ltd., Victoria, B.C.; accuracy ± 1 mm Hg, range 200 to 700 mm Hg) and applying calculations provided by Colt (1984). A tensionometer probe was mounted in the center of each of the three 0.74-m zones and oriented vertically on the downstream side of the aquarium. To minimize erroneous readings caused by bubble accumulation on the probe membrane the bubbles were dislodged by attaching the meter cables to a pulley system, which allowed the probes to be manually shaken prior to obtaining readings.

Overhead illumination of the WCS aquarium was provided by a metal halide light source (daylight spectrum) with seasonal photoperiod control. The light was distributed evenly on the water surface by use of a Light Pipe™ (TIR Systems, Ltd., Vancouver, BC). Illumination was regulated by the 24-h rotation of a perforated screen, which provided gradual changes in light entering the Light Pipe™ from the light source. Photoperiod was adjusted bi-weekly to simulate natural seasonal changes using nautical twilight tables provided by the National Research Council of Canada. Artificial photoperiod cycles ranged from 4.5 h dark: 19.5 h light (including two 4.5-h periods of twilight representing dawn and dusk) in June to 6.5 h dark: 17.5 h light in August. The aquarium was illuminated at night with near infrared lighting, by an alternative light source shone through a red filter (50% transmission at 695 nm and at 722 nm with the peak at 705 nm). Fish behavior and movements were continuously recorded by a high resolution

camera (Panasonic WV-1850, 800 lines) with peak sensitivity in the near infra-red, coupled to a closed circuit black and white time-lapse video recorder (Panasonic AG-6750, 400 lines) and high resolution video monitor (Panasonic WV-5470, 850 lines). Vinyl curtains to occlude extraneous light and disturbance enclosed the aquarium, lighting systems, and camera. The WCS apparatus was housed in a self-contained, sound insulated, temperature and humidity controlled building to reduce visual and acoustic interference to the fish.

RESEARCH DESIGN AND EXPERIMENTAL PROTOCOL

To optimize the research design and the eventual choice of 8 replicate experiments, power calculations (PC-SIZE, Version 2.13, Dallal) were applied to estimates of fish distribution in the WCS under isothermal and thermally stratified conditions, with and without the presence of food. The two main factors of food and temperature effects were to be examined with 6 comparisons selected to encompass a range of conditions experienced by the fish during each experiment. Paired samples were compared and estimated mean differences were provided. The standard deviation (S.D.) of the differences was estimated at 20% (based on an estimated S.D. of 16.6% in our original estimates, and calculated using the formula: variance (x-y) = variance x *2*(1 - corrected (x-y)), with an estimated correlation of 0.30, and the test of equality of means was at the 0.008 level of significance. Because 6 comparisons were identified a priori, Bonferroni corrections were made to maintain a family-wise error rate of 0.05. Hence the significance level for any test was at 0.008.

The experimental period was from May 30, 1997 to August 15, 1997 and during this time the test fish grew from 1.39 ± 0.36 g to 15.92 ± 3.80 g. Eight groups of twenty fish were tested throughout this period. Each group was observed for 5 consecutive days following a 2-d acclimation to the test apparatus. Groups, rather than individuals, were used because of the natural schooling tendency of chum salmon and the adverse effect that separation from conspecifics could have on behavioral responses (Ryer and Olla 1991; Davis and Olla 1992). For each test, 20 fish were randomly removed from the stock tank and placed in the WCS aquarium which contained air equilibrated seawater (10.2 ± 0.5 °C, 101.2 ± 1.8% dissolved oxygen, 99.9 ± 1.7% TGP; 27.4 ± 1.3 ‰ salinity). The fish were left undisturbed but fed to satiation using an automatic feeder for 2 d before observations began.

Fish were observed without disturbance through slits in the light-occlusion curtains, which provided a view of the plexiglass front of the aquarium. The nature of the experimental protocol required that the pre-established boundaries between the top (0.74 m), thermocline (0.09 m), and bottom (1.39 m) layers of the thermally stratified tank be visually delineated by lines of taut string across the front viewing glass. Time-lapse video recordings commenced 10 min prior to the first observation period following the 2-d acclimation, and continued to the completion of each of the 8 experiments.

Specific observation periods were chosen to assist in the characterization of the behavior of chum salmon under different experimental conditions. Each observation period consisted of 100 determinations of fish distribution in each of the top (0.74 m), thermocline (0.09 m) or bottom (1.39 m) zones of the aquarium. Positions of fish were observed and determined in real time, for

a schedule of 9 observation periods during the 5-d sequence of experimental events which alternated between morning and afternoon, under isothermal or thermally stratified conditions, with food present or absent (Table 1). Each group of fish was observed under baseline (isothermal) and experimental conditions, thereby serving as their own controls. Observers noting the number of fish present in the two least-occupied zones of the WCS, at 30 s intervals, during a 50-min observation period recorded vertical distribution of fish. Fish not counted by observers were assigned a position in the remaining zone, for a sum of twenty fish per reading. Using these numbers the average percentage of fish (arcsine-squareroot transformation) in each zone was calculated for comparative purposes between observation periods. The percentages of fish observed in the 3 zones at specific times during each experiment, together with the average values, are reported by Korstrom et al. (1998).

FEEDING IN A THERMAL GRADIENT

On Day 2 (isothermal) and Day 4 (thermally stratified) of the 5-d experimental period (afternoon observation periods), 1 g to 2 g of dry pellet feed (Moore Clarke, Vancouver, B.C., Nutra C starter feed #1) were added at the water surface, in the top zone of the aquarium. Feed was replenished on the water surface at 10-min intervals throughout the 50-min observation period without startling the fish.

SWIM SPEED

For each of the 8 behavioral experiments, the distance traveled, and swim speeds of each group of 20 randomly chosen fish were determined during each of the 9 observation periods. The trajectories of fish within the WCS aquarium were traced for a 30 s period on transparent Mylar sheets superimposed on the video monitor screen. The actual distance each fish traveled (cm) was calculated from correction factors based upon the dimensions of the WCS and the image reduction on the monitor. Swim speed over the 30 s period was calculated from the known distance traveled and was expressed in both absolute ($cm \cdot s^{-1}$) terms and relative to bodylength ($bl \cdot s^{-1}$).

EXCURSION TIMES

During afternoon observation periods, and under different experimental conditions, the time spent by individual randomly selected fish in the top zone of the WCS was determined with a stopwatch and recorded (s). The movement of fish into this zone was described as an excursion, and excursion times $\geq$120 s were assigned a duration of 120 s for subsequent use in data analyses.

TRANSITION TO THERMAL STRATIFICATION

On Day 3 of each experiment a thermal gradient was established between the top and 2 lower zones of the WCS aquarium, between the morning and afternoon observation periods. This thermal change resulted in the formation of a narrow, well-defined thermocline. The temperature

in the top zone was raised progressively through the continuous replacement of the 10 °C water with air-equilibrated 30 °C water (approximately 90% replacement time in 2.5 h at 20 $L \cdot min^{-1}$). The rate of change of temperature varied, becoming progressively slower over time, but the average rate of heating over the 4 h period was 0.06 $°C \cdot min^{-1}$. Data loggers recorded temperature every 15 min during this transition period and through to stable thermal stratification. After 4 h, temperature ranges for the 3 zones were top, 23.3 °C - 23.8 °C; thermocline, 13.7 °C - 22.8 °C; bottom 9.9 °C - 11.4 °C. Water in the middle and bottom zones of the WCS resisted downward heat transfer from the top zone due to constant chilling by recirculation through the closed loop refrigeration system. This protocol produced controlled and reproducible variation in temperature in the WCS aquarium, and provided a stable thermocline with the maintenance of two discrete, horizontally flowing water masses above and below, under continuous-flow conditions.

During establishment of thermally stratified conditions, observers noting the number of fish present in the two least-occupied zones of the WCS at 30 s intervals over the entire 4 h period regularly recorded the vertical distribution of the fish. Fish not counted by observers were assigned a position in the remaining zone, for a sum of twenty fish per reading. Using these numbers, the average percentage of fish in each zone during the transition of the temperature in the top zone from 10.2 ± 0.5 °C to 24.1 ± 1.4 °C could be examined. The fish count data for the 3 zones of the WCS aquarium were used in conjunction with temperature recordings from the top zone to examine the responses of the fish during this transition. The final temperature of the water above the thermocline was chosen to represent a level (potentially stressful to lethal based on previous laboratory research by Brett (1952)), that could be experienced by chum salmon in the Port Moody Arm of Burrard Inlet, especially close to the discharge of ≤27 °C heated cooling water from the electric-generating station, and locations further east towards extensive mud flats (Birtwell et al. 1998).

DIGITAL IMAGE ANALYSIS

The precise location of individuals and groups of fish was quantified from an analysis of videotapes, using a computerized image analysis system. The analog video images were captured by a video processor (PIP 640B Video Digitizer Board, Matrox Electronic Systems Ltd., Dorval, Que.) which is a "plug in" card that allows an IBM PC microcomputer to perform frame grabbing operations on a video signal from an external source. The computer software program "Snap" (Sci Tech Consultants Inc., Vancouver, BC) digitized the image of the fish on the video frame by transforming the x and y co-ordinates of each fish into graphic images that depict the school distribution. Subsequently, the program calculated statistical parameters for each image which included the center or mean of the distribution, the median value which gives some indication of the normality of the distribution, and standard deviational ellipse values which give a statistical indication of the shape of the fish school.

During experiment #5, seven randomly-chosen frames of video tape from each of the 9 observation periods were superimposed onto one composite graphical image and digitized to exemplify fish distribution under each stable isothermal or stratified condition. During the transition period, when the thermal gradient was being established in the aquarium, a composite

image of 7 randomly-chosen frames of video tape were digitized for each approximately 1 °C increase in temperature occurring in the top zone. For the purpose of image clarity, when overlaying multiple video frames onto a single composite image, only 7 frames were combined to illustrate the distribution during the selected time periods.

THERMAL RESISTANCE BIOASSAY

Apparatus

The flow-through bioassay apparatus consisted of six cylindrical insulated polyethylene tanks measuring 33.5 cm in diameter with water depth maintained at 34 cm by a central stand-pipe drain, providing a total water volume of 29.6 L. The tanks were covered with sheets of styrene-foam insulation to reduce heat loss, provide cover for fish, and reduce disturbance. Treatment water was supplied to 1 L reservoirs mounted in the tank covers. To facilitate mixing, water in the reservoirs was discharged through polyethylene tubing to the tank bottom and displaced water exited via the standpipe at the water surface.

Heated seawater was maintained in a large 2500 L insulated constant head reservoir. The water in this reservoir was cycled though a thermostatically controlled, counter-current titanium heat exchanger connected to a two-stage boiler system, which provided a continuous flow of water at a constant temperature. Heating of water in the closed system resulted in dissolved gas supersaturation (an elevation in total gas pressure (TGP) over atmospheric conditions). The supersaturated (109.1 ± 0.8% TGP), heated seawater (25.0 ± 0.3 °C) was delivered, as required, directly to the bioassay apparatus from the reservoir or was re-equilibrated to air saturation levels by diversion through an insulated, packed (2.5 cm Koch flexi-rings) column (Birtwell and Kruzynski 1987), which fractured and dispersed incoming water. The air-equilibrated (100.6 ± 0.6% TGP), heated seawater (24.9 ± 0.3 °C) exiting the column flowed into a 140-L constant head polyethylene tank and was subsequently distributed to the bioassay test tanks. During acclimation in the test apparatus, the bioassay test tanks were supplied with sand filtered, ambient temperature (10.8 ± 0.3 °C) air-equilibrated (98.9 ± 0.6% TGP) seawater pumped from an intake structure situated approximately 100 m offshore from the laboratory at a depth of 15 m below the low tide level. Temperature in the bioassay test tanks was recorded every 10 min by data loggers (Onset Stowaway Tidbit waterproof temperature logger, Onset Computer Corporation, Pocasset, MA, USA, ± 0.2 °C accuracy, -5 to 37 °C range).

Protocol

Eight thermal resistance bioassays were conducted between June 30, 1997 and August 15, 1997.

During the experimental period the juvenile chum grew and accordingly different sizes of fish were used (weight 4.0 ± 1.4 g to 19.1 ± 4.2 g; length 76.4 ± 9.4 to 123.6 ± 8.4 mm). Ten fish were randomly removed from the stock tank and transferred to each of the 6 bioassay test tanks containing air equilibrated 10 °C seawater. The fish were not fed and were left undisturbed to allow recovery from handling stress for 18 h prior to experimentation i.e. before increasing

temperature. All fish holding criteria were within standards established by Sprague (1973). Water flow during acclimation was delivered to the tanks at 2.5 $L \cdot min^{-1}$, which ensured a 90% replacement of the tank water volume within 1 h and provided a flow-loading of 0.08 $kg \cdot L^{-1} \cdot min^{-1}$. Fish density was maintained at ≤ 6.4 $kg \cdot m^{-3}$.

Following acclimation, duplicates of two treatments and controls were randomly assigned among the test tanks. Treatments comprised exposure to either supersaturated heated seawater (109.1 ± 0.8% TGP; 25.0 ± 0.3 °C) or air-equilibrated heated seawater (100.6 ± 0.6% TGP; 24.9 ± 0.3 °C). Control fish were supplied with air equilibrated ambient temperature seawater (98.9 ± 0.6% TGP; 10.8 ± 0.3 °C). Water flow was increased to 5 $L \cdot min^{-1}$ (99% replacement in 36 min) which facilitated a rapid transition to treatment water temperatures (0.4 $°C \cdot min^{-1}$) and ensured minimal heat loss from the test tanks.

Fish in the treatment test tanks were observed continuously, and the time to death of each fish was recorded. The bioassays were terminated when the last fish, exposed to either treatment, died. The standard behavioral criteria for stress at lethal temperatures described by Baroudy and Elliot (1994) included loss of equilibrium, sudden bursts of activity with frequent collisions with the container sides, followed by rolling and pitching with rapid ventilatory movements. However, for the purposes of this study, fish were considered dead when there was cessation of opercula movement. The control groups were simultaneously observed to assess any incidental mortality due to handling stress or exposure to laboratory conditions. The time to death of each fish was recorded from the time when the test tank water reached the target temperature of 24.5 °C, approximately 36 min after admission of treatment water.

The fork length (mm) and weight (g) of the 20 control fish from each bioassay were recorded. Dissolved oxygen concentration (Handy MKIII, Point 4 Systems, Port Moody, BC), salinity (YSI portable salinity meter, Yellow Springs Instruments Ltd., Yellow Springs, Ohio) and TGP (Model 300C Tensionometer, Alpha Designs Ltd., Victoria, BC, ± 1 mm Hg accuracy) values were measured at the conclusion of each test. Salinity ranged from 25-28 ‰ and dissolved oxygen concentration was 81.2 ± 4.7% and 96.5 ± 2.4% in the control and heated water treatment tanks respectively.

SUPPLEMENTARY EXPERIMENTS

In addition to the primary study, a brief preliminary and supplemental investigation was carried out using the WCS apparatus. On September 22, 1997, 20 juvenile chum salmon (weight 36.88 ± 8.54 g; length 154.60 ± 12.01 mm) were transferred to the WCS aquarium from the stock tank. Following 24 h acclimation in air-equilibrated seawater, live brine shrimp (*Artemia sp.*) were introduced to the top zone of the isothermal (10 °C) aquarium to determine if the hatchery-reared, pellet-fed fish would adapt to feeding on live prey. Aliquots of aerated seawater (Elite 800 air pump, Rolf C. Hagen Inc., Montreal, Que.) containing brine shrimp were metered through a valve and connecting tube from a 25 L polyethylene carboy, by the operation of a programmable timer (Cat. No. N1507, Noma Ltd., Scarborough, ON).

On September 24 and 25, 1997 the WCS aquarium was vertically stratified, and a temperature of 18 °C, 25 °C, or 30 °C provided in the top zone. This warmer water was separated by a thermocline from 10 °C deeper waters, as in the main experiments. These temperature regimes were examined sequentially over the 2-d period. To investigate the concomitant effects on fish behavior of exposure to elevated TGP (109.0 - 113.5%), air was injected (approximately 2 $L \cdot min^{-1}$) from a compressed air cylinder into waters in the PVC pipe upstream of the centrifugal pump which delivered water to the top zone of the aquarium. Entrainment of this air in the closed system supersaturated the recirculating water in the apparatus. During these preliminary experiments, dissolved oxygen, salinity, temperature and TGP were monitored. Feed (*Artemia sp.*) was presented to the fish in the top zone under each temperature regime. Vertical distribution of fish was recorded by observers noting the number of fish present in the two least occupied zones of the WCS at 15 or 30 s intervals during a 4, 6, 8, or 13 min observation period. The different duration of observations reflects the preliminary nature of this exploratory work. Fish not counted by observers were assigned a position in the remaining zone for a sum of twenty fish per reading. Using these numbers the average percentage of fish in each zone was calculated for comparative purposes between the temperature regimes.

RESULTS

THERMAL RESISTANCE BIOASSAYS

The short-term survival of chum salmon in heated seawater was examined from June to August to reveal any potential change in their acute lethal tolerance to 25 °C associated with the size and age of the fish, and to study the effects of TGP plus heat.

The time-mortality graphs for the combined data from 8 experiments followed the expected asymmetric sigmoid curve for each treatment group (Figure 2). There were no significant differences in the mean or median times to death of the salmon regardless of treatment (Table 2). The death of the first and last fish occurred at 50 min and 343 min respectively, in 25 °C water without elevated TGP. In 25 °C water with elevated TGP the first fish died at 65 min, and the last fish at 304 min. The loss of equilibrium immediately prior to death was noted but the onset of this behavior was not recorded. The control fish survived in all experiments.

The combined data for 8 experiments revealed that the median time to death was 150 min (95% confidence limits; 136 to 162 min), and 157 min (146 to 162 min) for chum exposed to 25 °C water with and without elevated TGP ($\sqrt{}$ 109.1 ± 0.8%). Respective mean values for times to death of fish exposed to 25 °C water with and without elevated TGP were 157.1 ± 46.8 and 159.0 ± 56.9 min.

WATER COLUMN SIMULATOR STUDIES

Figure 3 depicts the rate of temperature change in the top zone of the WCS aquarium as the tank became thermally stratified. Little variation occurred during all experiments as shown in

Table 3. The final stable structure provided a top zone (0.74 m depth) of the water column at a temperature of 24.1 ± 1.4 °C, which was separated by a narrow, well-defined and stable thermocline (0.09 m), from a deeper layer (1.39 m) of seawater in which temperatures ranged from 9.9 to 10.9 °C. The data for temperature, dissolved oxygen, salinity, and TGP are reported by Korstrom et al. (1998). The data reveal the lack of variation with time, and hence the stability of the varied, but controlled, conditions.

Influence of temperature rise and the presence of food in the surface waters of the WCS

Descriptive statistics

To determine if the presence of food or a rise in temperature of the waters above the thermocline affected the percentage of fish using this zone, the percentages of fish in the top zone when food was added to the surface waters without or with conditions of thermal stratification (isothermal vs isothermal + food; stratified vs stratified + food) were compared using a repeated measures analysis of variance (ANOVA), (Devore 1991). Table 4 reveals the mean, median and standard deviation, and percentage of fish for the combined data set (n = 8), over the 9 experimental observation periods and conditions.

The results of the repeated measures ANOVA determined that the percentage of fish in the top zone of the WCS was significantly different for both temperature change ($p < 0.001$) and the presence of food ($p = 0.001$). Fewer fish were in these waters at high temperature relative to the numbers of fish under isothermal conditions, and when food was present. The presence of food resulted in even more fish recorded in this zone, the greater number being present under isothermal, in contrast to thermally stratified and consequently higher temperature, conditions. However, the variable representing the interaction of food and temperature was not significant ($p = 0.650$): the percentage of fish in the top zone was significantly lower when the temperature was high, and the percentage of fish was higher when food was present.

Data for the percentage of fish recorded in the thermocline were analyzed similarly. The percentages of fish at the thermocline were significantly different for both the temperature change and the presence of food ($p < 0.001$) in surface waters. Contrasting with the waters above this zone, the percentage of fish increased in relation to temperature change in surface waters and with the presence of food there was a similar trend. The variable representing the interaction of food and temperature was significant ($p = 0.027$).

There was not a significant difference in the percentage of fish recorded below the thermocline due to temperature change in the top zone of the WCS ($p = 0.131$), nor with the presence of food in that zone ($p = 0.087$). Contrasting with the findings for the thermocline and waters in the top zone of the WCS, there was a significant ($p = 0.045$) interaction of food and temperature.

The results of these analyses imply that the effect of temperature on the percentage of fish in the top zone was independent of the presence of food. Contrasting with this was the significant interaction of temperature and food on the percentage of fish at the thermocline and in deeper

waters. When temperature was high in the top zone, the percentage of fish at the thermocline increased over isothermal (baseline) conditions. However, when food was also present in thermally-stratified conditions, the increase in the number of fish at the thermocline was not as large: fish which had aggregated at the thermocline in the absence of food, emigrated from this zone to feed in the overlying water. The results for the deeper waters show the opposite effect. Under conditions of thermal stratification the percentage of fish increased in the thermocline, and in the presence of food fewer fish occupied this zone and they were more dispersed into waters above and below. To examine these results in more detail a series of comparative statistical tests were carried out on the fish presence data at the previously mentioned observation periods (Table 1).

Comparative statistics

The experimental protocol permitted 6 comparisons of fish presence data (%) and swim speed, and 5 comparisons of the duration of time spent in the top zone of the WCS. To further examine the response of the fish to the imposition of heat and the presence of food under isothermal and thermally stratified conditions in the 3 vertical zones of the aquarium the data were compared using paired samples t-tests with a family-wise error rate of 0.05 (Devore 1991). We considered p values between 0.1 and 0.05 to be marginally significant in these comparisons, and are identified as such below.

To facilitate comparisons between the recorded statistics, the data that were collected for fish in the 3 zones of the WCS that were identified under thermally stratified conditions (top, thermocline, and bottom), were compared with the appropriate data collected from equivalent zones under isothermal conditions. That is, for example, the percentage of fish in the thermocline zone was compared with the percentage of fish that occupied the equivalent water volume and depth under isothermal conditions. The results of these statistical analyses are presented in Tables 5 to 7.

WCS top zone

i) ***the presence vs absence of food under isothermal conditions: afternoon determinations.***

A significant increase in the percentage of fish (from 27.4% to 62.0%) occupying the top zone of the aquarium was observed when food was presented in this zone (Table 5). At the same time their swim speed (Table 6) increased (4.0 $cm \cdot s^{-1}$ to 9.4 $cm \cdot s^{-1}$) but the duration of time spent in the top zone (Table 7) did not differ (>23 s). This latter statistic is limited by the arbitrary 120 s end to the observation period for those randomly chosen fish that did not move between zones. These fish were assigned a 120 s duration for the purposes of statistical comparisons. Thus, there is the distinct potential for an underestimation of the time spent in this zone under isothermal conditions, with and without the presence of food. At no time was this approach necessary under thermally stratified conditions because fish never stayed in the warmer water longer than 120 s.

ii) ***the effect of temperature under thermally stratified vs isothermal conditions: morning determinations.***

Relative to isothermal conditions, and the absence of food, a significant reduction in the percentage of fish in the top zone (33.0% to 4.3%) was observed with the imposition of heat to this zone. However, swim speed was not significantly different.

iii) the effect of temperature under thermally stratified vs isothermal conditions: afternoon determinations.

The effect of temperature on fish as deduced during afternoon observation periods, was similar to observations in the morning under the same conditions. Fish percentage in the top zone was reduced with the imposition of heat (27.4% to 2.2%), and swim speed was not changed. However, there was a significant reduction in the duration of time that fish spent in the top zone under thermally stratified conditions (23.3 s to 3.2 s).

iv) ***the presence of food vs absence of food under thermally stratified conditions: afternoon determinations.***

Contrasting with the thermally stratified situation and the absence of food, significantly more fish were observed using the top zone when food was present (an increase from 2.2% to 29.8%), despite the potentially lethal (~ 24 °C) temperature therein. Similarly, there was a significant increase in swim speed (4.0 $cm \cdot s^{-1}$ to 17.3 $cm \cdot s^{-1}$), and the time that fish spent in the heated waters was significantly elevated (3.2 s to 10.7 s), but not to the same level recorded under isothermal conditions when food was present (>23.3 s).

v) ***the presence of food under isothermal vs thermally stratified conditions: afternoon conditions.***

While the swim speed of the fish was elevated during the presentation of food under thermally-stratified conditions (17.3 $cm \cdot s^{-1}$ vs 9.4 $cm \cdot s^{-1}$), they used these waters for less time than under isothermal conditions (10.7 s vs >23.4 s). Although more fish occupied the top zone under isothermal conditions when food was presented (62.0% vs 29.8%), the difference was considered to be marginally significant.

vi) ***the presence of food under thermally stratified condition vs the absence of food under isothermal conditions: afternoon determinations.***

Relative to isothermal conditions and the absence of food, the presence of food under thermally-stratified conditions did not result in a significant difference in the respective percentages of fish (29.8% vs 27.4%) occupying the upper (~ 24 °C) zone. The duration of time spent in the top zone during conditions of thermal stratification and in the presence of food was shorter than that during isothermal conditions (10.7 s vs 23.3 s). As expected, the swim speed of the fish in the former situation was significantly faster (17.3 $cm \cdot s^{-1}$ vs 4.01 $cm \cdot s^{-1}$).

WCS thermocline

Only 2 comparisons of percentage fish data (Table 5) for this zone, among the conditions identified above, were considered to be marginally significant [$p \leq 0.1$; comparisons i) and vi)], while the remaining 4 comparisons were significant ($p \leq 0.05$).

i) ***the presence vs absence of food under isothermal conditions: afternoon determinations.***

The percentage of fish in this zone was reduced when food was presented in the overlying waters (6.6% vs 16.9%). The result was marginally significant and reflects the response of the fish to food and the associated increase in the percentage of fish in the top zone.

ii) ***the effect of temperature under thermally stratified vs isothermal conditions: morning determinations.***

Consistent with the reduction in the percentage of fish in the heated (~24 °C) waters above the thermocline relative to isothermal conditions, there was a significant increase in the percentage of fish that were recorded in the thermocline (15.4% to 66.6%).

iii) the effect of temperature under thermally stratified vs isothermal conditions: afternoon determinations

The same response noted for comparison (ii) above, in the morning observation period, was recorded during the afternoon in this comparison. Significantly more fish were in the thermocline than in the same zone of the WCS under isothermal conditions (69.1% vs 16.9%).

iv) ***the presence of food vs absence of food under thermally stratified conditions: afternoon determinations.***

Significantly fewer fish occupied the thermocline when food was presented in the very warm (~24 °C) waters above (31.4% vs 69.1%). This response was mirrored by a corresponding increase in fish in the top zone during feeding.

v) ***the presence of food under isothermal vs thermally stratified conditions: afternoon conditions.***

Significantly more fish were present in the thermocline when food was added to the ~24 °C surface waters under conditions of thermal stratification, than under isothermal conditions (31.4% vs 6.6%). The result contrasts with the same comparison made in the top zone (see WCS top zone, v) above), reflecting the mediating effect of temperature on feeding in surface waters.

vi) ***the presence of food under thermally stratified condition vs the absence of food under isothermal conditions: afternoon determinations.***

Although more fish (31.4% vs 16.9%) were recorded in the thermocline during the presentation of food in the heated waters above, relative to cooler isothermal conditions, the result was considered to be marginally significant ($p \leq 0.1$).

WCS bottom zone

In the deeper waters below the thermocline zone, comparisons iv) and v) below, of fish presence data (Table 5), were not significant, while all others were deemed to be marginally significant ($p \leq 0.1$).

i) ***the presence vs absence of food under isothermal conditions: afternoon determinations.***

Fewer fish were in these deeper waters when food was presented in the top zone (31.5% vs 55.8%), reflecting the feeding response and the occupation of shallower waters.

ii) ***the effect of temperature under thermally stratified vs isothermal conditions: morning determinations.***

More fish were in the deeper and cooler waters (at acclimation temperature) under isothermal conditions in contrast to the thermally stratified situation (55.8% vs 29.1%), when the majority of the fish were in the thermocline.

iii) the effect of temperature under thermally stratified vs isothermal conditions: afternoon determinations

As for the same comparisons made on data from the top zone and the thermocline, regardless of time of day, there was a similar response of the fish to thermal stratification, and a result very similar to that in comparison ii) above was obtained. More fish were present in the bottom zone under isothermal conditions than under conditions of thermal stratification (55.8% vs 28.7%).

iv) ***the presence of food vs absence of food under thermally stratified conditions: afternoon determinations.***

There was no significant difference in the number of fish in the bottom zone during the presentation of food in the top zone, under thermally stratified conditions.

v) ***the presence of food under isothermal vs thermally stratified conditions: afternoon conditions.***

As for comparison iv) above, there was no significant difference in the percentage of fish in the bottom zone irrespective of isothermal or thermally stratified conditions and the presentation of food from the water surface.

vi) ***the presence of food under thermally stratified condition vs the absence of food under isothermal conditions: afternoon determinations.***

There was a higher (marginally significant; $p \leq 0.1$) percentage of fish in the bottom zone of the WCS under the baseline isothermal conditions than under conditions of thermal stratification and the presentation of food (55.8% vs 38.8%).

Baseline condition comparisons

Comparisons were undertaken among the baseline isothermal observation periods 1, 3, 5 and 9 (see Table 1), to determine if the vertical distribution of the fish differed throughout the experiment. This was a precautionary step taken because of the sequential nature of the tests and the possibility that the behavior of the fish in successive and different conditions could be influenced by prior events. Periods 1, 3 and 5 were before thermal stratification, and 9 was afterwards. The results of pair-wise comparisons using a 2-tailed Students' t-test did not reveal a significant difference among the baseline conditions that the fish were exposed to ($p \leq 0.05$).

Location of individual chum salmon and the school under isothermal and thermally-stratified conditions, with and without the presence of food

Figures 4 to 12 present the results of a series of digital image analyses from Experiment 5. A spatially orientated boundary representing the 95% confidence limits around the mean fish position was drawn around the school. The digitized images show the exact position of each fish in the aquarium and provide a more precise description of their vertical distribution within the WCS. The images contrast with the coarser determinations of fish location, which were assigned to the top, thermocline and bottom zones of the aquarium. Because of the consistency in the response of the fish to the imposed conditions, we considered that it was appropriate to characterize and exemplify the response by reference to one experiment. Each of the images support the conclusion of the statistical analyses detailed previously. However, the comparative statistical analyses reported above provide a more rigorous and complementary assessment of the fish distribution data among top, thermocline and bottom zones of the WCS.

Under isothermal (baseline acclimation) conditions the school of chum salmon was biased towards the water surface and most often occupied the left side of the aquarium. The fish were frequently orientated towards the incoming water (3-5 $cm \cdot s^{-1}$), and the median position was close to that of the thermocline under stratified conditions. Figures 4, 5 and 6 show a range of positions of individual fish and schools during the morning baseline periods before thermal stratification occurred. Figure 7 shows the distribution at the same time of day upon return to isothermal conditions following thermal stratification. The images are not strictly comparable because of the sequential changes that occurred prior to these images being captured. They do, however, reveal the extent of variation that occurred, which was minimal on experimental days 1 and 2, increased on day 3 following feeding the previous afternoon and evening, and was similarly high on day 5 following thermal stratification and feeding.

The images presented in Figure 8 contrast markedly with those in Figures 4, 5, 6, and 7, and show the response to thermal stratification, and the occupation of the thermocline by most of the fish.

The images captured from afternoon observation periods show the effects of thermal stratification with and without the presence of food, and contrast with previous images obtained for observation periods in the morning. Figures 9, 10, 11, and 12 show the position of fish under isothermal, isothermal plus food, thermal stratification and thermal stratification plus food conditions, respectively.

Figure 9 depicts the position of the fish in the afternoon of day 1 under isothermal conditions, and contrasts with the position of fish at the same time of day under thermally stratified conditions (Figure 11). Under the latter conditions the majority of the fish were at the thermocline. Although the median position of the fish school moved marginally downwards relative to the position under isothermal conditions (Figure 9), the school was less dispersed and orientated horizontally. This shift to the relatively small volume of the thermocline zone indicated the volitional actions and thermal choice of individual fish to occupy waters intermediate in temperature from those below (at the previous acclimation temperature of ~ 10 °C) and those above (at ~24 °C). A few fish were recorded away from the school and the possibility exists that the thermocline zone presented an unacceptable level of confinement to some individuals even though behavioral thermoregulation appeared to occur.

The distribution of fish under isothermal conditions and in the presence of food is illustrated in Figure 10. In contrast to the images of fish during the same isothermal situation, but without food (Figure 9), these images show the increased dispersion of the school and the location of individuals both closer to the tank bottom and water surface (from where the food was presented on the left side of the aquarium). Under these circumstances the chum salmon were often widely dispersed and used all depths of the aquarium. The ellipse representing confidence limits of the mean and the school orientation shows this relative dispersion and the almost vertical orientation of the school to the water surface from whence the food came.

When food was presented under thermally stratified conditions (Figure 12), the school was relatively dispersed but orientated towards the water surface and the entry place of food. The relatively brief time that the fish spent in the potentially lethal surface waters to feed and their increased swim speed could have contributed to the change in orientation of the school and individuals. The majority of fish remained close to the thermocline, but more dispersed than when food was absent. The dispersion is likely associated with the response to food overriding the behavioral thermoregulatory response and the avoidance of elevated (~24°C) temperature, both of which would favor long-term survival.

Acute response to elevated TGP and feeding on live prey at 18 °C, 25 °C, and 30 °C

A brief 2-d investigation examined the responses of chum salmon to the presence of food and TGP. The results of these trials are shown in Table 8, together with relevant water characteristics. Prior to starting these tests the fish were provided with brine shrimp (*Artemia sp.*) to determine if they would readily convert from feeding on an artificial diet to capturing live prey. The fish quickly fed upon the brine shrimp, reinforcing the opinions of Paszkowski and

Olla (1985), and Stradmeyer and Thorpe (1987), regarding the feeding success of hatchery reared fish previously fed artificial diets, on natural live prey.

Under isothermal conditions (9.8 to 10.1 °C), 65% of fish occupied the top zone. With an increase in the temperature in the top zone to approximately 18 °C there was a corresponding shift in their vertical distribution. In contrast to the situation when the above-thermocline waters were at ~24 °C, 87% of chum salmon occupied the top zone at 18 °C.

To ascertain any effects of short-term exposure to elevated TGP levels in the top zone, it was necessary to choose a temperature that the fish would occupy. It was also important to ensure stratification in the water column through sufficient density differences and not compromise the structural integrity of the horizontally flowing water layers. The introduction of air into the waters entering the top zone resulted in an elevation of TGP (111.0% to 113.5%), and, coincidentally, numerous bubbles. Because of the shallow water depth the hydrostatic pressure was insufficient to maintain the gasses in solution.

The response of chum salmon to the imposition of elevated TGP for 2.5 h in the top zone of the WCS at 18 °C, had little discernible effect on the use that the fish made of these waters over a short period of time. In an 8 min observation period (n = 17 observations), 66% of fish were in the top zone, similar to pre-stratified conditions. When live *Artemia sp.* were added just below the surface of the water, feeding occurred, with a corresponding increase in the number of fish in the top zone.

Subsequent elevation of the top zone temperature to 25 °C resulted in the previously reported avoidance response of the chum salmon to occupy deeper waters, away from the potentially lethal conditions. The majority of the fish were in the thermocline. The elevation of TGP for 30 min, and the associated bubbles of air in these waters, followed by the introduction of live food, resulted in an increased occupancy of, and feeding in, the top zone. This response was similar to that recorded in the absence of elevated TGP (with artificial food) in the primary experiments. The chum salmon fed actively in the waters with elevated TGP and over a 13-min observation period (n = 34), a mean of 51% of fish was recorded in these waters.

When the temperature of the top zone was elevated to 30 °C (plus elevated TGP for 2.5 h), the fish avoided this zone and remained in the cooler, deeper waters of the thermocline and below. The introduction of *Artemia sp.* into the top zone stimulated feeding. The fish made transient excursions to feed in the 30 °C waters even though it was > 6°C higher than the ultimate lethal level of 23.8 °C determined by Brett (1952). The 30 °C waters were approximately 15 °C higher than the preferred temperature deduced from our experiments, and 5 °C higher than that temperature (i.e. 25 °C) shown in this study to result in the death of juvenile salmon if exposure to this elevated temperature was sustained for more than 50 min. The fish exited the top zone rapidly after a brief period of feeding (seconds), and frequently penetrated to the cooler (10 °C) sub-thermocline waters. Over a 6-min observation period (n = 17 observations) a mean of 32% of fish were present in these waters; 19% and 34% less than in waters at 25 °C and 18 °C, respectively.

Because of the trial nature of these temperature and TGP variations, it would be unwise to draw conclusions. It is obvious, however, that the fish did not display any marked aversion to the short-term exposure to elevated TGP, and feeding occurred in waters at 25 °C and 30°C. There is an indication from the distribution data that fewer fish were present in the top zone in the presence of food at 30 °C than at 25 °C or at 18 °C. This may also be a reflection of the relative time that each fish would spend in the lethal waters. Although no determinations were made of the time that an individual spent in these waters, it appeared that it was shorter at 30 °C than at 25 °C and there was an increase in the distribution of fish throughout the water column.

Behavioral response of chum salmon to temperature during a change from isothermal to thermally-stratified conditions

General trends

A severe lightning storm prevented data from being gathered during this phase of one of the experiments; hence the reduction in replicates relative to other study components.

The introduction of air-equilibrated warm seawater at a fixed rate into the top zone of the WCS aquarium resulted in a progressive increase in temperature and the development of thermal stratification. During this thermal change the position of the school of fish changed and revealed three distinct phases. During the initial temperature rise in surface waters, individuals in the school became closer and the population tended to shift upward to occupy positions in the top zone of the aquarium, proximal to the water surface. As the temperature continued to rise there was a period when the majority of fish occupied the waters above the thermocline, but this was followed by a progressive downwards movement and the school tended to occupy the narrow thermocline rather than the larger volume of deeper waters at the acclimation temperature (10 °C). This occupation of the thermocline by the majority of fish persisted throughout 24 h of thermal stratification but was temporarily affected by the presence of food in the waters above, as previously described. This general behavioral trait in response to the development of thermally stratified waters occurred in each of the experiments, with fish of different ages and sizes. On occasion the school dispersed into 2 or more smaller units.

Behavioral observations of individual fish interactions were occasionally recorded. It appeared that agonistic behavior was minimal when the fish were smaller but aggressive behavior (nipping, chasing) was noticed towards the end of the experimental period under isothermal conditions when the fish were substantially larger.

Distribution and statistical analysis

During the transition phase the majority of change associated with the fish distribution occurred in the uppermost part of the water column (top zone and thermocline regions). Accordingly, attention was devoted to the number of fish in these water bodies for the data analysis. Our objective was to develop a model that captured the relationship between number of fish and temperature. Linear and non-linear regression analysis was applied to the top zone data

where the main temperature change took place. Data for the thermocline was also modeled to verify the top zone model results. All data were used for these analyses: no outliers were omitted in an attempt to minimize internal error.

Fish presence in the surface waters (top zone) during transition to thermally stratified conditions

A non-linear relationship between percentage of fish and temperature was suggested following a review of the data for individual experiments. For exploratory purposes a stepwise polynomial model was used to fit the data, and, the step-wise regression results selected a second order (quadratic) equation (Systat 1992). While this model fit the data, our knowledge of fish behavioral thermoregulation and thermal preference suggested that the model should reveal 3 phases representing an initial movement to preferred temperatures, a zone of thermal preference (and a focus on temperatures that bound this range) and a phase representing the avoidance of high temperatures. Accordingly, a 3-segment piece-wise non-linear regression was selected and run for all data and each experiment.

The initial "attraction" phase was described by: $y = (a1*T + a2)$, for temperature greater than 10 °C, and less than the lower boundary "preferred" temperature range. The preferred temperature range, between 2 boundary temperatures was of the form $y = (a4)$. Following this phase an "avoidance" relationship was described by the form $y = (a5*T + a6)$.

The 3-phase model to be estimated was:

$y = (a1*T + ((-a1)*k1 + a4))*(T > 10 \text{ and } T < k1) + (a4)*(T >= k1 \text{ and } T <= k2) + (a5*T + ((-a5)*k2 + a4))*(T > k2)$.

In this model y = percentage of fish, T = temperature of the top zone, k1 and k2 are estimates of the lower and upper temperature parameters of the "preference" phase, and a1, a4 and a5 are parameter estimates in the "attraction", "preference" and "avoidance" phases, respectively. Parameters a2 and a6 are redundant, because to keep the model continuous at the lower and upper temperatures, the intercept of the "attraction" and "avoidance" phases were defined as a function of the other parameters.

To select starting points for the parameters in the piece-wise non-linear regression, the fish percentage data were divided to sets below and above 16 °C. Linear regressions (fish percentage vs temperature) provided the slope of the relationship, and the resulting coefficients were used as starting points for the parameters (a1 and a5) in the non-linear model.

The results of the piece-wise regressions applied to the percentage of fish in the top zone of the WCS for the individual (n = 7), and combined experiments, are shown in Table 9. The results reveal a good fit overall, but a slight non-linear relationship for the residuals in the "avoidance" phase of the model was suggested as the fish moved deeper in the water column to primarily occupy the thermocline. The results of the regression analyses applied to the data sets are shown in Figure 13, (parameter a1 = 23.1, k1 = 13.7, a4 = 83.5, k2 = 17.9, a5 = -14.7, R^2 = 0.684).

To test the robustness of the model, the regressions were estimated for the data set minus the data for one experiment; each of the data for one experiment was removed in turn to estimate the values of the model parameters (k1, k2 , a1, a4, and a5). The results (Table 10) show only a marginal shift in these estimates from those of the full data set (the variation in k1 and k2, the boundaries to the "preferred" temperature range, were the least sensitive to the removal of data).

The data analyses revealed the responses of chum salmon to thermal change and defined temperatures selected and avoided during this time. The acute thermal preference of 50% of the fish (EC50) lay between 12.2 °C and 20.2 °C (determined from the piece-wise regression analysis), but a narrower range was identified in which >83.5% of the fish occupied a temperature range of 13.7 °C to 17.9 °C (values k1 and k2 of the model, respectively; Tables 9, 10, and Figure 13).

Chum salmon elicited avoidance responses to increasing temperatures in the top zone by moving downwards in the water column. The temperature of 17.9 °C (k2, Tables 9, and 10; refer to Figure 13) provides an inflection point after which less than 83.5% of the fish were in the top zone. Numbers of fish continued to decline in the top zone with a corresponding increase in the thermocline and, to a lesser extent, the deeper and cooler waters below. The mean temperature at which 50% chum salmon avoided rising temperature and entered the thermocline was 20.2 °C, with 90% avoidance occurring at 22.9 °C (Figure 13).

Fish presence in the thermocline zone during transition to thermal stratification

A regression model was estimated for the thermocline zone of the water column during the imposition of heated water to the top zone to determine if fish behavior was consistent with that revealed for the waters above. The fish displayed the 3 behavioral tendencies of "attraction", "preference" and "avoidance" to the changing temperatures of the top zone surface waters during the establishment of thermal stratification, and a tendency to occupy the thermocline as temperatures increased in shallower waters above. This trait is consistent with "behavioral thermoregulation" whereby the fish tends to occupy waters in which temperatures are in an optimum range for metabolic and physiological processes (Brett 1971). Accordingly, it was expected that the general distribution shifts of fish that were observed in the top zone of the WCS would be mirrored by similar, but opposite, changes in fish presence in the thermocline. This would be especially noticeable during the "preference" and "avoidance" phases when fish were moving to the shallower waters of the warming top zone and subsequently avoiding these waters as temperatures continued to increase. Data for all experimental periods were combined for the regression analysis with the following results: parameter a1 = -4.02, k1 = 13.6, a4 = 3.27, k2 = 17.4, a5 = 11.87, R^2 = 0.76, and the graph fitted to the data is presented in Figure 14.

At the start of the transition to thermal stratification the variation in the percentage fish data shown in Figure 14 relates to the general movement of the schooling fish as they became more active and occupied the warming surface waters above the thermocline zone. The data reveal a temperature range between 13.6 °C and 17.4°C when 96.8% of fish did not occupy the

thermocline zone. This compares favorably with the preference range of 13.7°C - 17.9 °C for occupation of the top zone by 83.5% of the fish under these conditions. Thus, the absence of the majority of fish in the thermocline zone was reflected by a corresponding presence of fish in the shallower and warmer waters. As the temperature in the top zone surface waters continued to rise (beyond 17.4 °C) more fish exited the surface waters and began to occupy the thermocline, as revealed by the regression analysis. The occupation of the thermocline was favored over the cooler deeper waters, at the acclimation temperature. The EC50 level for fish entering the thermocline in response to increasing surface temperatures was 21.3 °C contrasting with the EC50 response value of 20.2 °C for chum salmon movement from the increasing surface water temperatures of the top zone. This difference was likely related to the variation in the numbers of fish moving to occupy not just the thermocline but the deeper cooler waters below, in contrast to the more precise movement of fish from the top zone as temperatures increased to ~24 °C.

Location of individual chum salmon and the school during the thermal transition period

The location of individual fish in the aquarium through the transition from an isothermal to a thermally stratified water column, during Experiment 5, is shown in a series of sequential images (Figures 15 to 28). The 7 randomly chosen video frames per digital image were selected for each consecutive, approximately 1 °C interval, during the temperature rise, to show the progressive, yet rapid and consistent response of the chum salmon to thermal change.

The median position of the school of chum salmon during the rise from 10 °C to 12 °C lay around the position that the thermocline would occupy under stratified conditions (Figures 15 and 16). However, between 12 °C and 13 °C (Figure 17) there was a significant upward shift by the school to utilize the upper zone of the WCS. The median school position remained close to the surface during increasing temperatures (13 °C to 18 °C) in the upper zone even though the dispersion of individuals varied widely and encompassed the total water column (Figures 18 - 22). Between 18 °C and 20 °C the median position of the school shifted downwards towards the thermocline, but individual fish continued to utilize the whole water column (Figures 23 and 24). Fewer fish were in the upper, or lower, zones of the water column when the temperature was between 20 °C and 21 °C. Individual fish tended to be closer together than at lower temperatures and the median school position was at the thermocline (Figure 25). Most of the fish were schooled at and around the thermocline when the waters above were at 21 °C to 22 °C (Figure 26). This pattern was persistent and the median school position remained at the thermocline as temperatures continued to slowly increase towards 23.7 °C (Figures 27 and 28). Fish made transient excursions above and below the thermocline and those into the potentially thermally lethal surface waters were rapid.

DISCUSSION

Juvenile chum salmon of different age displayed similar responses to the imposition of heat in seawater. They preferred waters that were warmer than acclimation temperatures and avoided temperatures which, according to Brett (1952) and the present thermal resistance studies,

approached or exceeded threshold levels that could prove acutely lethal to these fish if exposures were continuous for ≥50 min. When provided with a choice, the fish displayed thermoregulatory behavior that could be temporarily disrupted by the motivation to feed, even in waters that were potentially lethal to them. These results were consistent over the 11 week experimental period.

We endeavored to provide thermal conditions in our experiments that could occur in the marine waters of Port Moody Arm, Burrard Inlet. The temperatures chosen as the upper limits were 24 °C to 25 °C. Although a temperature of 27 °C is permitted in the cooling waters discharged from the BGS, we chose a lower temperature because of the modeled dissipation of heat in Port Moody Arm, and anticipated maximum values in these receiving waters. Predictions by Seaconsult Marine Research Ltd. (1995) indicated that the discharge of 27 °C water would result in an elevation of 1 °C to 1.5 °C, to 2 °C to 3 °C over ambient summer temperatures in the surface 4 to 5m depths under maximum operating conditions and the discharge rate of 1.7×10^9 $L \cdot d^{-1}$ and 2.5×10^9 $L \cdot d^{-1}$, respectively. Ambient maximum surface water temperatures of 22 °C have been recorded in Port Moody Arm. A further increase in temperature for these waters of only 2 °C to 3 °C would create conditions that could prove acutely lethal to underyearling chum salmon if they remained in the warm (≥24 °C) thermal plume associated with the BGS heated cooling water discharge for periods of an hour or more. The extent of this temperature increase could occur over approximately 40% of Port Moody Arm, (Seaconsult Marine Research Ltd. 1995). Furthermore the temperature of waters within an initial (100 m) mixing zone were predicted to be 5 °C to 6 °C higher than ambient by the effluent surface water "boil" close to the outfall (Seaconsult Marine Research Ltd. 1995). Accordingly, the selection of temperatures between 24 °C and 25 °C was deemed appropriate for use in our experiments. Additional relevance was provided through the use of chum salmon from the local Seymour River at a time when they would be found (March to August) in the marine waters of Burrard Inlet (Macdonald and Chang 1993). Chum salmon are the most prevalent salmonid in the area (Macdonald and Chang 1993), and also the least tolerant of the Pacific salmon species to high temperature (Brett 1952).

THERMAL RESISTANCE

The experimental protocol we chose to examine the resistance of chum salmon to temperature resulted in a rapid increase in temperature from ambient seawater acclimation levels (around 11 °C) to 25 °C. The technique differed from that used in direct transfer experiments (e.g. Brett 1952) which limits acclimation and measures mortification (Kilgour and McCauley 1986), and from slow heating experiments that measure both mortification and partial acclimation. The latter technique is most useful in the determination of the upper ultimate incipient lethal temperature or critical thermal maximum (Becker and Genoway 1979). If the rate of heating is rapid, the results of tolerance tests can be skewed upwards due to the delay required for internal core temperatures to match ambient values (Becker and Genoway 1979; Kilgour and McCauley 1986). Coutant (1977a) however, comments that any rate of temperature change that is applied over minutes to hours will not greatly affect the thermal tolerance limits because acclimation takes more time. Ideally the change in temperature from baseline values should proceed at a rate that permits the equilibration of tissue temperature with ambient temperatures while at the same time being fast enough to prevent acclimation (Houston 1982). Spigarelli et al. (1974) found that

the internal temperatures of fish abruptly exposed to a temperature elevation of 4 °C to 9 °C differed from ambient values in proportion to body weight: internal temperatures stabilized in 10 min for fish <100 g, and within about 1 to 2.5 h for larger fish (approx. 4000 g). Similar lag times were recorded by Spohn et al. (1996) who inserted temperature-transmitting ultrasonic tags in the stomachs of adult sockeye salmon. It is not surprising therefore, that the use of relatively high rates of temperature change in laboratory tolerance tests result in differing critical thermal end points (Bell 1973; Vanderhorst et al. 1974; Young and Apts 1973). These end points tend to be higher than the upper lethal limits determined using techniques relying on abrupt temperature changes, such as occurred in the thermal resistance bioassays (Brett 1952, Konecki et al. 1995).

The overall rate of heating in our thermal tolerance experiments was 0.4 °C·min^{-1} prior to attaining 25 °C. This rate is marginally greater than the 0.3 °C·min^{-1} recommended by Becker and Genoway (1979) for evaluations of critical thermal maxima, and substantially different than the 6 °C·min^{-1} used by Vanderhorst et al. (1974), and Young and Apts (1973).

THERMAL RESISTANCE AND TGP

The median resistance times to 25 °C water for chum salmon were 150 and 157 min in seawater with and without elevated TGP at 109%. These results compare favorably with those obtained by Brett (1952) who examined the resistance of juvenile salmon to temperature in fresh water. Because thermal tolerance and resistance is intimately influenced by prior thermal history, comparisons between experimental data sets should only be made between results for fish acclimated to the same temperature, and in this instance, 10 °C. Brett (1952) determined that the median resistance time for fresh water acclimated chum salmon was 160 min at 25 °C, and 900 min at 24 °C. The resistance times increased substantially at higher acclimation temperatures, rising to 700 min and 4260 min at acclimation temperatures of 15 °C and 23 °C, respectively. The onset of death was preceded by loss of equilibrium, a feature that could render the fish susceptible to predation in the natural environment (Coutant 1973). In the present studies, the first fish died at 50 min in waters at air saturation and at 65 min in the supersaturated conditions. These differences in the time to death of the first and last (304 - 343 min) fish between treatments are considered to be insignificant, a result that is not surprising considering that the time required for the death of fish at elevated TGP (in the absence of thermal stress) is usually hours to days depending on saturation level (Meekin and Turner 1974). These authors report that juvenile chinook salmon and steelhead trout could withstand 16 h exposure to 135% nitrogen supersaturation. However, their tests were conducted with dissolved oxygen levels less than 100%. In tests involving supersaturation of oxygen and nitrogen (116% and 124%, respectively), chinook, coho and steelhead died quicker than at similar nitrogen levels (122%). This suggests that both dissolved gasses contribute to the mortality of the fish. The bioassays we undertook were at lethal temperatures, and we anticipated that the combined thermal and TGP stress would result in different resistance times between the two treatments. That this did not occur may be a function of the rapidity of the test and the variance in the data obtained. The experiments of Meekin and Turner (1974) were conducted at constant, relatively low temperatures (around 10 °C - 12 °C), contrasting with our experiments. Ebel et al. (1971) concluded that an increase in temperature over ambient would be detrimental to migrating juvenile salmonids during periods of nitrogen supersaturation. It cannot be ruled out, therefore, that at highly stressful temperatures

concomitant elevated TGP levels, especially of nitrogen and oxygen, would create additional stress on fish in contrast to any factor acting alone. It is perhaps such an event that resulted in the death of juvenile salmonids during summer (1997) in the Bridge River, British Columbia (B. Antcliffe, Department of Fisheries and Oceans, Vancouver, B.C., pers. comm.). Spillage of water from a dam was considered to elevate TGP and, although at relatively low levels (<105%), the combined effects of warm water and the absence of deep refugia to compensate for elevation in TGP (Ebel 1969, Shrimpton et al. 1989) over a prolonged period could have acted synergistically and fatally.

Irrespective of the lack of difference in the results under contrasting levels of dissolved gas saturation, the median resistance times for chum salmon in seawater determined in this study compared favorably with determinations made by Brett (1952) for this species in fresh water. The closeness of the median resistance times determined by Brett (1952), to those determined in this study, were unexpected considering the differences in the size (54.3 to 56.4 mm to 76.4 to 123.6 mm, respectively) and ages of the fish used and the different osmotic conditions between fresh and salt water. However, Brett did not find a relationship between mortality and size in the tolerance of higher temperatures (in low temperature tolerance studies the smaller fish died first). Similarly, Bidgood and Berst (1969) found that size did not affect the tolerance of rainbow trout (*Oncorhynchus mykiss*) to upper lethal temperature. Contrasting with these findings, however, Beacham and Withler (1991) determined that heavier chinook salmon survived better in thermal tolerance experiments than lighter individuals in seawater. As the median resistance times determined for chum salmon in seawater were very close to those recorded by Brett (1952) in fresh water, we could not discern any potential effect of osmotic change in this instance. Brett (1952) indicated the potential interaction of thermal and osmotic stresses, and the increased thermal resistance of Atlantic salmon in salt water versus fresh water supports this view (Alabaster 1967).

The upper temperature that we chose to use in the examination of chum salmon behavior was just higher than the upper lethal limit for juvenile chum salmon in fresh water, as determined by Brett (1952). He determined that the upper lethal temperature for chum salmon acclimated to 10 °C was 22.6 °C and that the ultimate upper lethal limit was 23.8 °C. A range of 15 °C in acclimation temperature from 5 °C to 20 °C only resulted in an upward change of 1.9 °C in the upper lethal limit (Brett 1952). Recent work on the tolerance of chinook and coho salmon suggests that different results could be obtained through genetic (Beacham and Withler 1991), and phenotypic variation (Konecki et al. 1995), respectively. Although the latter authors state that their results of critical thermal maxima exceeded published data from some laboratory tests (of lethal limits), their methodology was different, and so was the result. They established a critical thermal maximum for different coho salmon removed from streams of differing temperatures. While their results have relative value, and reveal the advantage of acclimation in the wild to the tolerance of elevated temperatures, they also reflect the expected higher thermal end point determined by the critical thermal maximum test (over the upper lethal temperature determined via a different method and for a different purpose). To this extent, the results of Konecki et al. (1995) do not refute the earlier work of Brett (1952), DeHart (1975), and McGeer et al. (1991) but expand our knowledge of potential thermal tolerance in field situations.

Beacham and Withler (1991), who speculate that the upper lethal temperatures for a salmonid species may be more population-specific than previously realized also share this opinion.

BEHAVIORAL THERMOREGULATION AND ACTIVITY IN ISOTHERMAL AND THERMALLY STRATIFIED SEAWATER

We chose to examine the behavior of chum salmon to temperature change in the vertical plane, thereby providing a degree of relevance to vertical stratification that occurs in natural marine coastal waters. At the same time, the WCS apparatus provided an opportunity to follow the associated changes in responses of the fish as thermal stratification occurred and temperatures rose to 24 °C. To this extent the changes simulated, on a very small scale, the initial introduction of the BGS's heated cooling waters into the marine environment of Port Moody Arm.

An examination of the experimental techniques by which to examine thermal choices by fish resulted in the conclusion of McCauley and Pond (1971) and McCauley (1977), that the nature of the gradient in the apparatus plays a lesser role than generally believed in influencing laboratory findings. Furthermore, results obtained through the use of vertical and horizontal gradients were similar, and more variance was likely because of non-thermal factors such as age, size, season, physiological and pathologic condition, and social factors (McCauley and Pond 1971; Giattina and Garton 1982).

The effects of hydrostatic pressure and fish distance from the water surface are potentially confounding variables in vertical distribution studies, but these were eliminated from concern by the earlier work of Brett (1952). By varying the thermal gradient in a small aquarium he was able to show how the response of fish followed the gradient and was independent of depth. Such findings have been reinforced in subsequent studies in the laboratory and field. Thus we consider that the WCS apparatus that permitted the manipulation of thermal gradients in the vertical plane was both appropriate and relevant to the examination of the thermal responses of chum salmon in marine waters.

Isothermal conditions

Groups of experimental fish placed in the WCS were allowed approximately 60 h to recover from the stress of handling, and adjust to, and explore, their new environment before their distribution and behavior were examined. After acclimation, we determined that the fish were located in the upper part of the 2.4 m isothermal water column and biased towards the surface. The fish were generally in one school and their activity level was quite low. Most fish were orientated into the flow of incoming water at 3 to 5 $cm \cdot s^{-1}$ and their overall mean swim speeds were 4.0 to 4.6 $cm \cdot s^{-1}$ (0.5 to 0.6 $bl \cdot s^{-1}$). The salmon spent at least 23 s in the 0.74 m top zone on the aquarium, but were constantly moving. Social interactions were noticeably more agonistic as the fish became larger and more confined by their surroundings (especially when densities increased in the thermocline as they responded to the thermally stratified conditions). Ryer and Olla (1996) also noted agonistic behavior by chum salmon in the absence of predators but in the presence of dispersed (but not clumped) food. The presence of predators did not prevent

agonistic behavior when food was clumped and dominant fish monopolized it. When food was dispersed in the presence of predators, agonistic behavior ceased.

Despite the different conditions that the fish experienced during each of the 5-d experiments in this investigation, "baseline" fish distribution before, versus after, periods of introduction of food and thermal changes, was not significantly different. This result implied that the fish rapidly recovered from the experimental manipulations during each experiment, and that their behavior (distribution) subsequently and quickly returned to those recorded under isothermal baseline conditions.

The shallow surface water orientation of underyearling chum salmon has been observed in the wild through detailed underwater observation, fishing, and experimental cage studies. Observation and capture of, and experimentation with, chum salmon in the wild confirm the relatively shallow habitats occupied by this species during their early sea life. Macdonald and Chang (1993) collected underyearling chum salmon in shallow beach seines close to shore in Burrard Inlet. Mason (1974) observed chum salmon in shallow waters (<1 m) of a coastal stream and estuary, and both Beak Consultants Ltd. (1981) and Healey (1982) caught juvenile chum salmon in shallow waters in the estuaries of the Fraser and Nanaimo Rivers, respectively. Macdonald et al. (1987), using underwater observations, also documented the shallow-water habitat of salmonids in the Campbell River estuary. Birtwell and Harbo (1980), McGreer and Vigers (1983), and Birtwell and Kruzynski (1989), using an experimental in-situ cage technique, determined that the volitional distribution of juvenile chum salmon resulted in the occupation of the upper 1 m of marine waters during their early sea life (a position that was changed through avoidance to pulp mill effluent). In the most recent studies that employed the same experimental technique in the waters of Port Moody Arm, chum salmon displayed the same behavioral tendency to occupy surface waters (Birtwell et al. 1998). At later stages in their life, chum salmon occupy a much greater range of depths in marine waters. In off-shore waters in the Gulf of Alaska, Manzer (1964) found no conclusive evidence regarding the vertical distribution of chum salmon (of different sizes and ages >1^{+} to 4 years) and temperature, although at night they were always caught above the thermocline (June and July). Because of these findings, the vertical distributions observed in the WCS are considered to be highly representative of that which may occur in nature under similar situations.

Response to thermal change and stratification

Chum salmon respond to progressive thermal increase from isothermal to thermally stratified conditions by shifts in distribution and activity changes. These movements to occupy a particular temperature range reflect the opportunity for behavioral thermoregulation, and the associated optimization of metabolic functions (Brett 1971; Coutant 1975; Fry 1975; Magnuson et al. 1979, Reynolds and Casterlin 1980; Coutant 1987). The acclimation temperature of 10 °C used in the present behavioral trials was below that determined to be preferred by this species in fresh water (Brett 1952). Accordingly, when heated water was admitted to the WCS resulting in a warming of the uppermost (0.74 m) layer, the fish responded by entering these waters. With progressive increases in the temperature of the surface waters to 24 °C, the fish distribution shifted downwards and the median school position was at the narrow thermocline. Interestingly, the fish

chose to utilize the thermocline more than the cooler waters below, to which they had been previously acclimated. These distribution shifts of the school followed a pattern of thermal recognition and choice. They chose to enter into waters of a particular temperature range, and subsequently avoided increasing temperatures as they rose to potentially lethal levels. These acute responses of the fish to thermal choices conform with the behavioral thermoregulatory responses of many other fish (e.g. Brett 1952; Sullivan and Fisher 1953; Fry 1975; Cherry et al. 1975, 1977; Spigarelli et al. 1983), and add to the extensive literature on the temperatures preferred and avoided by fish (e.g. Cherry et al. 1975; Coutant 1977b; Houston 1982).

Thermal preference and regulatory behavior

In these behavioral trials, chum salmon in seawater displayed an acute preference for temperatures ranging between 13.7 °C and 17.9 °C, with an EC50 within the range of 12.2 °C to 20.2 °C. Most individuals chose to occupy the thermocline (temperature range 22.8 °C to 13.7 °C) during stable conditions of thermal stratification. The only other published work on the thermal preference of chum salmon was reported by Brett (1952), who examined their response in fresh water in the late evening using low intensity lighting illuminating the side and middle of a 0.9 m-deep, 420-L aquarium. Brett determined that the mode of preferred temperatures of juvenile chum salmon lay between 14 °C and 15 °C irrespective of prior acclimation to temperatures of 10 °C, 15 °C, or 20 °C. However, mean (± S.D.) preferred temperatures were 13.9 ± 1.1 °C, 14.1 ± 1.0 °C and 14.6 ± 1.3 °C, for fish acclimated to 10 °C, 15 °C, and 20 °C, respectively. In this study we used an aquarium that was almost 11-fold larger (4500 L), illuminated from above to simulate daylight conditions with photoperiod control, which provided a continuous-replacement, flow-through seawater environment. Thus we attempted to mimic some of the cues found in natural marine waters. Our observations were conducted during standardized daytime periods and we used fish of significantly larger size range than did Brett (1952). These factors, coupled with the different experimental protocols, could have been associated with the small difference in mean results between our respective studies.

The results that we obtained for the acute thermal preference of chum salmon encompassed, but were over a greater and higher range of temperatures than, the mean and modal determinations of thermal preference determined by Brett (1952). Within the range of temperatures selected by chum salmon the mean value was 15.8 °C (EC50 range) to 16.2 °C (EC83.5 range: maximum response determined from piece-wise regression analyses); these temperatures were very close to those considered to be optimal for the physiological performance of Pacific salmon (Brett 1971). Our determinations were approximately 1 °C higher, while Brett's determinations were approximately 1 °C lower, than the optimal 15 °C performance level (based primarily on the energetics of sockeye salmon). Considering variation among lethal and sublethal responses of individuals, populations, and species to temperature (Konecki et al. 1995; Beacham and Withler 1991; McGeer et al. 1991), the thermal preference determinations by Brett and ourselves revealed behavioral thermoregulatory responses of chum salmon that were proximal to those temperatures considered to optimize physiological performance. This result is in accordance with the expectations from other studies and the opinion that the final temperature preferendum of a fish relates to efficient metabolic function (Brett 1971; Coutant 1977a).

The final temperature preferendum is the temperature around which fish aggregate given an opportunity to do so in a gradient of sufficient extent (Fry 1947). The acute thermoregulatory response is defined as the clustering of individuals, or of occurrences of a single individual about some particular temperature (Fry 1975). The acute and final thermal preferenda are, therefore, separated through time. Our experiments provided information on the acute thermal preference of chum salmon acclimated to 10 °C. The thermal preferendum can be elevated by such factors as starvation (Javaid and Anderson 1967), physiological activities (Crawshaw 1977), prior thermal history (Reynolds and Casterlin 1980), age (Kwain and McCauley 1978), and infections (Reynolds et al. 1976), but not to circadian activity (Reynolds 1977), aside from mediation by non-thermal factors (Giattina and Garton 1982). Most of the intrinsic factors can be eliminated as significant influences on the results we obtained. The fish were free of disease, in good nutritional state (fed the day prior to thermal changes), acclimated to 10 °C (a factor that did not result in significant variation in the preferred temperature of chum salmon in Brett's (1952) work), but were of different ages (significant differences among experiments were not evident). Accordingly, we consider that the results have validity and are representative of the choices that chum salmon make in thermal seawater gradients under laboratory conditions: choices that could be affected by other factors in the wild.

The significance of the preferred temperature range and behavioral thermoregulation lies in the potential exploitation of habitats and niche selection, and the maximizing of metabolic and physiological functions that have adaptive and survival value (Coutant 1975; Reynolds and Casterlin 1976; Coutant 1977a; Crawshaw 1977; Reynolds 1977; Magnuson et al. 1979; Giattina and Garton 1982; Spigarelli et al. 1983). Chum salmon would be expected to occupy temperatures between 13.7 °C and 17.9°C in marine waters, based on our results. This selection would, of course, be subject to modification by other factors. Because of this, Coutant (1977a) suggested that the temperature for optimum physiological and ecological performance would lie between the physiological optimum and the ultimate upper incipient limit.

Avoidance of heated seawater

In each of the 8 behavioral trials chum salmon avoided rising temperatures in increasing numbers as temperatures rose to potentially lethal levels in surface waters. The avoidance response of 50% of the test fish occurred at a temperature of 20.2 °C, and only 10% of fish were recorded at 22.9 °C. Coincident with the movement of salmon from the increasing temperatures of the surface waters was an increase in numbers at the thermocline. Some fish penetrated the thermocline to the deeper waters at the acclimation temperature, but the majority of fish aggregated at the thermocline in a relatively close school. The response of the chum salmon to move to, and occupy, the thermocline was positively related to the increasing temperature of the surface waters. The response was consistent in all 8 experiments and permitted the derivation of the 50% response level at 21.3 °C.

There is no similar information on the temperature that juvenile chum salmon will avoid with which to compare this result. However, Brett (1952) provided information on the upper lethal temperature limit for this species in fresh water. He determined that the ultimate upper lethal temperature limit was 23.8 ± 0.4 °C. This level is where acclimation to higher temperature has

no further effect on the raising of the thermal limit; acclimation temperature has been found to influence the thermal tolerance (and preference) of fish to this ultimate lethal limit (Brett 1952). As the chum salmon in our experiments were acclimated to 10 °C, the upper lethal temperature would be expected to be 22.6 °C as determined by Brett (1952). At 15 °C the limit was 23.1 ± 0.4 °C. Over an acclimation range of 13 °C (10.0 °C to 23.0 °C), the upper lethal temperature only increased by 1.2 °C. It is not unexpected, therefore, that individual chum salmon in the test population displayed avoidance behavior at temperatures much lower than 22.6 °C, and above the upper limit of the preferred temperature range (17.9 °C).

Gray (1990) investigated the avoidance response of juvenile chinook salmon in a raceway to simulate the discharge of heated water into a riverine situation. Although the temperature causing avoidance increased with acclimation temperature, the mean difference between that causing avoidance and ambient level was 9 °C to 11°C. Contrary to some findings in the field (when other cues, such as food, will exert an effect), Gray (1990) found no evidence of thermal attraction. Thus it was concluded that juvenile chinook encountering low temperature discharges in nature (< 9 °C above ambient) may orientate to, and remain in low velocity discharge currents: the consequences of such occupation being detrimental if combined with other stressors.

INFLUENCE OF TEMPERATURE AND FOOD ON THE DISTRIBUTION, SWIMMING, FEEDING AND USE OF SURFACE WATERS

In the present studies juvenile chum salmon schooled around the thermocline and generally avoided shallower waters when the aquarium was thermally stratified by a layer of warm, and potentially lethal, seawater (~24 °C) overlying cooler waters at the acclimation temperature (10 °C). Both temperature and the presence of food had a significant effect on the percentage of fish in the top zone and the thermocline. There was no similar effect on the presence of fish in the deeper, sub-thermocline waters. Thus, the effect of temperature on fish presence in the top zone was independent of the presence of food, whereas at the thermocline when the temperature was high the number of fish increased. When food was present with a temperature increase in the top zone, the increase in the number of fish was not as great. In the sub-thermocline zone, fish numbers decreased as temperature increased, but in the presence of food at such times the numbers decreased in response to feeding activity. The fish displayed behavioral flexibility and the effects of a non-thermal factor (food) temporarily modified the behavioral thermoregulatory response to occupy temperatures intermediate between those which were potentially lethal and those to which they had initially been acclimated.

Under isothermal conditions, fish activity was less and the school more dispersed. The presence of food stimulated feeding and there was a significant increase in the numbers of fish in surface waters, and in their swim speed. In the absence of food, the response of the fish to conditions of thermal stratification and potentially lethal conditions in the surface zone did not differ between morning and afternoon observation periods, leading us to conclude that their response was consistent throughout the daytime. Under these conditions, there was avoidance of potentially lethal temperatures and a significant reduction in the numbers of fish in surface waters. This corresponded with the significant increase in the number at the thermocline that chose to occupy these waters where temperatures occurred within their preferred range. Even though the waters above the thermocline were at levels that would likely have led to the death of

salmon over time given their previous acclimation history and continuous exposure to these conditions to ≥1 h, some fish continued to move into these waters from the thermocline, but for very short (3.2 ± 3.3 s) excursions.

The addition of food to the warm (~24 °C) surface waters resulted in a significant 14-fold increase in the numbers of fish using these waters, a 4-fold increase in their swim speed, and a tripling of the time spent in these waters. However, the fish did not spend as much time feeding in these warmer waters as they did under isothermal conditions. In the sub-thermocline waters, the results reflect the stimulation of temperature which prompted the fish in surface waters to move downwards to the thermocline under conditions of thermal stratification, and also their dispersion during feeding. Feeding in the 24 °C waters resulted in the fish occupying a larger part of the water column, and presumably, the need to seek, at least for brief periods, cooler waters after brief excursions into waters that were potentially lethal to them over time if they remained therein; thereafter, the fish aggregated at the thermocline.

The responses of chum salmon that we recorded in the laboratory were similar to general trends that have been observed in the field for other species of fish, albeit in freshwater environments. For example, studies on the distribution of fish around thermal discharges have revealed the attraction of fish to thermal discharges at certain times of the year, consistent with the optimization of metabolism. Elser (1965) reported that fishing (especially for catfish) in heated water was better during the cooler 9 months of the year than in the 3 summer months, implying attraction to warmer waters. Neill and Magnuson (1974) recorded concentrations of fish around a thermal discharge, but the distributions did not reverse with season or time of day, and were related to body temperatures of fish and their thermal preferences. Similarly, Kelso and Minns (1975) reported that a thermal plume had little effect on pelagic fish and speculated that the fish were either not available to the elevated temperatures or they failed to respond to increased surface temperatures. However, in later studies Spigarelli (1975) reported that rainbow trout were in thermal discharges for variable periods of time. This finding supports the seasonal changes in fish populations in reference and thermal plume areas, reported by Spigarelli et al. (1982). They found numbers of fish in the plume area to be up to two orders of magnitude greater than in cooler reference areas during late spring and early summer. Thereafter, the reference areas had a maximum of 10 times the numbers of fish in the plume location during late summer and early fall. Because of thermal preferences, large numbers of predatory salmon were in the thermal plume at times of low food densities. This "impoverished energetic situation" for the salmon within the plume was considered to be offset at a distance from the discharge by the high numbers of forage fish prey. The adaptation to thermal discharges is revealed by Spigarelli and Thommes (1979) who determined that the body temperature of fish increased with the thermal discharge temperature. Maximum body temperature exceeded the ambient temperature by 10 °C, while the population mean differed by 2 °C to 6 °C. Unlike the studies on chum salmon these results reveal the integration of temperatures experienced by the fish, and provide less insight into temporary use of waters at elevated levels. That fish were captured with body temperatures exceeding ambient by up to 10 °C, implies longer residence than we recorded for chum salmon in 24 °C to 30 °C waters. Thus fish have been documented to utilize thermal plumes and to distribute themselves according to thermal preferences.

ACUTE RESPONSE TO ELEVATED TGP AND FEEDING ON LIVE PREY AT 18 °C, 25 °C, AND 30 °C

Chum salmon were offered live prey (*Artemia sp.*) during a preliminary study to assess whether elevation in TGP above saturation levels and temperatures of 18 °C, 25 °C, and 30 °C affected presence in surface waters and feeding. The response was similar to that reported herein during conditions of thermal stratification and the presence of food. Neither elevation of TGP to 111% to 113% nor a temperature of 30 °C had a discernible effect on the feeding of juvenile chum salmon. The fish entered waters that were approximately 6 °C higher than the upper lethal limit of 23.8 °C determined by Brett (1952), and approximately 15 °C above the temperature considered to be physiologically optimal (Brett 1971). In experiments similar to these with chum salmon, Olla et al. (1985) examined the effect of cold temperatures and the presence of food in vertical gradients on a marine fish species "blue fish" (*Pomatums saltatrix*). These researchers also found that the fish responded to the introduction of thermally different water with increased swim speed and an upward shift to more favorable temperatures, in their case this was from increasingly colder to warmer waters. They also noted that the motivation to feed modified the avoidance response and the fish successfully fed in the cold water.

SWIM SPEED

The swim speed of chum salmon in the WCS experiments varied substantially and significantly among the various treatments, with most differences related to both temperature change and the presence of food. Although burst speed is independent of temperature (Brett 1971), lesser swim speeds in warmer waters will utilize more energy to a physiologically optimum temperature value. Pursuit speeds for chum salmon (30 to 70 mm) feeding on plankton were up to 15 $cm \cdot s^{-1}$, but mean speeds of 8 $cm \cdot s^{-1}$ were recorded for fish of 60 - 63 mm length (Wissmar and Simenstad 1988). Similar mean swim speeds (9.4 ± 3.8 $cm \cdot s^{-1}$) were recorded for chum salmon feeding under isothermal conditions in the WCS. However, during conditions of thermal stratification and feeding in waters with temperatures above their lethal limit (based on the determinations by Brett (1952), the salmon swam at a mean speed of 17.3 ± 5.9 $cm \cdot s^{-1}$, thus briefly exceeding the maximum pursuit speed recorded by Wissmar and Simenstad (1988). In our experiments, the fish generally moved a relatively short distance from the thermocline to feed in the overlying 0.74 m surface water zone. That they did this at a swim speed in excess of maximum pursuit speeds recorded for chum salmon feeding under less rigorous conditions implies that the ~24 °C temperature of the upper zone in the WCS stimulated this response. It is expected that feeding in such a manner in nature, in potentially greater volumes of water above preferred temperature levels, may be costly and increase energy demands: this demand increases exponentially with size because of the metabolism body weight - swim speed relationship (Wissmar and Simenstad 1988).

USE OF "SUB-OPTIMAL" WATERS

In our studies, the feeding of juvenile chum salmon in surface waters at temperatures from 24 °C to 30 °C did not result in the death of any chum salmon, despite repeated excursions. There are few records of fish dying during feeding experiments involving exposure to temperatures

higher than lethal tolerance limits. Neill and Magnuson (1974) in their comprehensive examination of the effects of thermal discharges on freshwater species of fish in the laboratory and in the field, state that thermoregulatory behavior of fish was not permanently overridden by feeding behavior. Even though planktonic food was more abundant in the thermal outfall area fish would only make brief feeding forays into these waters with extreme temperatures. However, in the laboratory, temperature limited the acquisition of a maximum daily meal, and as recorded in the present studies for chum salmon, yellow perch (*Perca flavescens*) spent significantly less time (<5%) in waters above their lethal limit and the duration of forays became <30 s. Two fish died during feeding experiments in which the perch obtained food in waters 3 °C above the upper lethal limit. Similarly, Munson et al. (1980) recorded the death (50% to 65%) of rainbow trout feeding in temperatures above the lethal limit. The fish were habituated to feeding at the end of a 2.4 m channel in which a thermal gradient occurred, with food being provided in the hotter waters. In waters that were from an acclimation temperature to 30 °C to 36 °C (up to 24 °C above acclimation temperature), some of the fish died while attempting to feed. Complete inhibition of motivation to feed was not achieved. Thus the motivation to feed, even in potentially lethal waters, overrode the expected thermoregulatory response. These findings are in contrast with the conclusions of Neill and Magnuson (1974).

It is not known whether feeding in waters at temperatures that are just above lethal limits, or above those optimal for physiological and metabolic function, has a detrimental effect on survival. Clearly, if exposure to elevated temperatures results in prolonged stress, inefficient utilization of energy, reductions in growth, increased risk of predation and disease, then the advantages of obtaining food are minimal. Studies by Greenbank et al. (1998) on the growth of juvenile chum salmon in dilutions of cooling water from the BGS determined that the fish grew at a slower rate in the warmer waters. Wissmar and Simenstad (1988) state that the metabolic costs of maintenance are in delicate balance with food intake and growth. If food was impoverished in the preferred, yet thermally heated surface waters, the energetic costs of capture in high temperature waters could limit growth. Donaldson and Foster (1941) found that juvenile sockeye salmon refused to feed when temperatures increased from 17.2 to 25.6 °C, but resumed feeding when temperatures returned to 21.1 °C. Similarly, Brett et al. (1982) found that 19 °C was the optimum temperature for the growth of juvenile chinook salmon fed on maximum ration, but above this level feeding and growth decreased. They also state that at 60% of maximum daily ration, the optimum temperature for growth decreased to 14.8 °C. Their studies did not permit opportunity for the fish to balance the thermoregulatory requirements against the energetic and metabolic demands of feeding and growth. Accordingly, feeding in higher temperature waters may not be as detrimental in thermally stratified environments that permit fish to thermoregulate and maximize performance. In this context, the movement of sockeye salmon into warmer surface waters to feed followed by a return to colder waters in lakes, is considered to be adaptive and energetically advantageous (Biette and Geen 1980). This apparent advantage is attributed to the lower maintenance requirements at colder temperatures and a concomitantly greater proportion of food available for conversion to growth (Brett 1971).

While the dispersion of food in the wild is unlikely to be available only in the surface waters (1 -2 m) where the juvenile chum salmon prefer to reside, their presence there suggests proximity to food. It has been suggested by Coutant (1987) that there may be marked differences in feeding

behavior in steep gradients and that fish may feed on uncharacteristic prey. Spigarelli and Thommes (1979) documented the reduced growth and condition in ictalurids due to strong thermal attraction and inadequate food in "thermally-enriched" areas. However, Spigarelli and Smith (1976) found no evidence of such an effect on rainbow trout from thermal plume and reference areas implying an ample supply of food for "plume-resident" fish. Quite obviously there are site-specific differences among the reported findings, but the pattern of attraction of fish to thermal discharges at certain times of the year is common to all.

Chum salmon are opportunistic and selective predatory sight feeders, which consume a variety of items that reflect abundance in fresh and salt waters (Higgs et al. 1995). If upper surface waters exceed preferred temperature levels due to the discharge of heated waters, reduced abundance in these waters may occur as the fish move to optimize metabolic function. Nevertheless, motivation to feed, in addition to responding to other cues will, seemingly, not prohibit occupancy for brief periods. The field experiments of McGreer and Vigers (1983) and Birtwell and Kruzynski (1989) determined that caged juvenile chum salmon may succumb to conditions in vertically-stratified waters where lethal conditions persisted close to the water surface; a result which is similar to that reported by Munson et al. (1980). Prolonged occupancy in waters heated above ambient could be detrimental through exposure to elevated levels of TGP. The mortality of Atlantic menhaden in the thermal plume of a nuclear power plant was related to elevations in TGP and the thermoregulatory responses of the fish which chose to occupy the plume region (Marcello and Fairbanks 1974).

The effects of thermal change on juvenile chum salmon in Port Moody Arm would be expected to follow a seasonal trend. In the spring there could be an attraction to, and occupancy of, waters at the preferred temperature, followed by a movement from increasing temperatures during summer. The timing and duration of these events would be related to many factors in addition to the discharge of heated water from the BGS.

SUMMARY AND CONCLUSIONS

The response of chum salmon to thermal change and food followed a trend that has been recorded for fish proximal to thermal plumes and during other laboratory investigations. That is, fish were attracted to waters of a particular temperature range, avoided higher temperatures, and were motivated to feed in waters with temperatures which approached or exceeded those which could be acutely lethal if exposure was sustained.

Based on this information, the temperature of waters in which this species resides during their early sea life would be expected to be less than those that induced thermal avoidance behavior. Temperatures would be below ~20 °C, and most probably <18 °C, (the 50% avoidance response level, and the upper limit of the preferred range). The preferred temperature range in seawater for this species and life stage would lie, approximately, between 14 °C and 18 °C, and favor optimal metabolic and physiological functions. Behavioral thermoregulation would be expected to favor survival, and the broader the range of the preferred temperature, the greater the scope for

exploiting habitats. Similarly, the greater the resistance to temperatures outside this range, the higher the opportunity for extending this range into "sub-optimal" regions for transitory and important activities such as feeding. In this regard, chum salmon displayed behavioral flexibility and showed that they are capable of briefly using waters approximately 6 °C and 15 °C higher than their lethal limit and optimum, respectively, in order to feed.

The consequences of the behavioral traits demonstrated in these studies to the survival of chum salmon in the waters of Port Moody Arm are not known with any degree of certainty, although they may be speculated upon based on this knowledge, and that from other research on thermal discharges. In the marine environment, the imposition of thermal regimes elevating temperatures above ambient to those in the preferred range would be expected to encourage fish occupancy from cooler waters; a situation that could occur in the spring and early summer. Assuming adequate food supplies, these conditions would favor growth (survival), but at the same time extended residence could result in exposure to elevated TGP if and when such conditions were present. This latter effect may be mediated behaviorally through the occupation of deeper waters, but this would remove the fish from their preferred surface water habitat.

Increasing the temperature of the surface waters of Port Moody Arm above the preferred range would be expected to result in their avoidance by juvenile chum and other species of salmon, as temperatures approached potentially lethal limits, typically in summer when fewer juvenile salmon are present. However, the innate behavioral trait to occupy surface waters during estuarine residence and early sea life may compromise survival if other non-thermal cues were dominant factors. In this circumstance, they could override thermal stimuli that would otherwise favor survival and the optimization of metabolic and physiological functions. Although chum salmon demonstrated an avoidance of potentially lethal high temperatures in the laboratory, they were also motivated to feed in such waters (to 30 °C). To this extent we do not know the effects of repeated excursions into waters that are potentially lethal, nor the consequences of longer occupancy of waters that may be stressful at the sub-lethal level (combined effects of temperature and elevated TGP; refer to Birtwell et al. (1998) on the health and performance of individuals and the link to survival.

The intermittent operation of the Burrard Generating Station would impose a similarly fluctuating thermal regime in Port Moody Arm because of the rapid (1 to 2 d) tidal-induced replacement of water (Waldichuk 1965). Such a scenario would probably reduce potential impacts on chum salmon during the early spring and summer, but might increase the risk of adverse effects such as thermal shock in winter and temporary habitat displacement in summer. Thus, the judicious discharge of heated cooling water could favor salmonid survival during spring and early summer if other environmental factors (biological, physical, and chemical) were appropriate for maintaining health and performance.

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Table 1. Schedule of nine 50 min observation periods during each five day experiment.

Observation Period	Day	Time	Conditions	
			Temperature	Feeding
1	Monday	AM	Isothermal	no Food
2	Monday	PM	Isothermal	no Food
3	Tuesday	AM	Isothermal	no Food
4	Tuesday	PM	Isothermal	Food
5	Wednesday	AM	Isothermal	no Food
6	Wednesday	PM	Stratified	no Food
7	Thursday	AM	Stratified	no Food
8	Thursday	PM	Stratified	Food
9	Friday	AM	Isothermal	no Food

Table 2. Summary of time to death data for juvenile chum salmon exposed to heated sea water at air saturation and at supersaturation.

Date	Bioassay #	Conditions	Time to Death (minutes)						Total Gas Pressure
			Mean	SD	Median	Min	Max	n	(% TGP)
30-Jun	1	Heat	109.6	26.0	113.5	50.0	157.0	20	100.1
30-Jun		Heat + TGP	102.3	18.5	104.0	65.0	132.0	20	108.8
21-Jul	2	Heat	173.9	27.7	178.0	124.0	219.0	20	100.5
21-Jul		Heat + TGP	247.1	56.0	234.5	156.0	343.0	20	107.4
24-Jul	3	Heat	141.5	34.7	145.0	65.0	190.0	20	100.4
24-Jul		Heat + TGP	138.7	19.8	135.5	102.0	171.0	20	109.6
28-Jul	4	Heat	118.7	29.7	111.0	82.0	185.0	20	101.9
28-Jul		Heat + TGP	105.2	22.5	97.5	70.0	155.0	20	109.3
1-Aug	5	Heat	153.7	42.4	149.5	93.0	300.0	20	100.2
1-Aug		Heat + TGP	138.0	30.5	135.5	95.0	218.0	20	108.9
5-Aug	6	Heat	164.7	30.7	164.5	118.0	219.0	20	100.6
5-Aug		Heat + TGP	157.4	34.4	151.0	119.0	264.0	20	109.9
12-Aug	7	Heat	170.6	29.0	169.0	76.0	220.0	20	100.8
12-Aug		Heat + TGP	180.6	33.2	178.0	97.0	238.0	20	109.9
15-Aug	8	Heat	224.9	40.4	231.0	160.0	304.0	20	100.0
15-Aug		Heat + TGP	203.0	38.0	201.5	138.0	282.0	20	109.2

Bioassay #	Condition	Time to Death						TGP (%)	
		Mean	SD	Median	Min	Max	N	Mean	SD
1 - 8 combined	Heat	157.2	46.8	157.0	50.0	304.0	160	100.6	0.6
1 - 8 combined	Heat/TGP	159.0	56.9	150.0	65.0	343.0	160	109.1	0.8

Table 3. Determination of temperature (mean ± SD) during the transition to thermally stratified conditions in the WCS aquarium during experiments 1 - 8.

TIME		TEMPERATURE (°C) Data Logger Number TOP #1	TOP #2	TOP #3	TOP #4	THERMOCLINE #5	THERMOCLINE #6	THERMOCLINE #7	THERMOCLINE #8	BOTTOM #9	BOTTOM #10	BOTTOM #11	BOTTOM #12
Logger Depth (cm from surface)		16.5	36.5	54.5	74.5	84.5	88.0	90.5	94.0	122.0	151.5	191.5	238.8
9:15	MEAN	10.1	10.2	10.2	10.2	10.3	10.2	10.3	10.2	10.3	10.2	10.0	9.8
	SD	0.2	0.2	0.2	0.2	0.1	0.2	0.2	0.2	0.1	0.1	0.1	0.1
9:30	MEAN	11.4	11.4	11.4	11.0	10.8	10.6	10.7	10.6	10.6	10.5	10.1	9.8
	SD	0.5	0.4	0.4	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.1
9:45	MEAN	13.3	13.3	13.1	12.2	11.5	11.3	11.3	11.2	10.9	10.8	10.2	10.0
	SD	0.5	0.5	0.5	0.4	0.3	0.2	0.2	0.2	0.1	0.2	0.1	0.1
10:00	MEAN	14.7	14.7	14.5	13.6	12.9	12.6	12.4	12.0	11.1	10.9	10.2	10.0
	SD	0.8	0.9	0.8	1.0	1.0	0.9	0.7	0.6	0.3	0.4	0.2	0.2
10:15	MEAN	16.0	16.0	15.8	15.1	14.4	13.9	13.4	12.6	11.2	11.0	10.2	10.1
	SD	1.1	1.1	1.1	1.3	1.4	1.2	1.0	0.4	0.5	0.5	0.4	0.4
10:30	MEAN	17.3	17.3	17.2	16.4	15.7	15.1	14.3	13.2	11.2	11.0	10.1	10.0
	SD	1.1	1.1	1.1	1.3	1.4	1.3	0.7	0.5	0.5	0.6	0.4	0.5
10:45	MEAN	18.4	18.4	18.3	17.7	17.0	16.3	15.0	13.6	11.3	11.1	10.1	9.9
	SD	1.1	1.1	1.1	1.1	1.3	1.0	0.6	1.0	0.6	0.6	0.4	0.5
11:00	MEAN	19.4	19.4	19.3	18.7	18.0	17.1	15.3	13.8	11.3	11.1	10.1	10.0
	SD	1.1	1.0	1.1	1.1	1.2	1.0	0.6	1.3	0.6	0.6	0.3	0.4
11:15	MEAN	20.1	20.2	20.1	19.5	18.8	17.9	15.7	13.8	11.4	11.1	10.2	10.0
	SD	1.0	1.1	1.1	1.2	1.2	0.9	0.9	1.5	0.6	0.6	0.3	0.4

Table 3. (cont.)

		TEMPERATURE (°C)											
		Data Logger Number											
		TOP				THERMOCLINE				BOTTOM			
TIME		#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12
11:30	MEAN	20.8	20.8	20.7	20.2	19.5	18.5	15.9	13.8	11.4	11.1	10.2	10.1
	SD	1.1	1.1	1.1	1.1	1.2	0.9	0.9	1.3	0.7	0.5	0.3	0.4
11:45	MEAN	21.3	21.4	21.3	20.7	20.0	19.0	16.1	13.8	11.4	11.2	10.2	10.1
	SD	1.1	1.0	1.1	1.1	1.2	1.0	1.0	1.2	0.6	0.5	0.3	0.3
12:00	MEAN	21.8	21.8	21.8	21.2	20.6	19.5	16.5	13.8	11.4	11.3	10.2	10.1
	SD	1.0	1.1	1.0	1.1	1.2	1.1	1.1	1.0	0.7	0.6	0.2	0.3
12:15	MEAN	22.2	22.3	22.1	21.7	21.0	19.9	16.5	13.6	11.4	11.2	10.2	10.1
	SD	1.0	1.0	1.0	1.1	1.2	1.1	1.1	1.0	0.6	0.6	0.2	0.3
12:30	MEAN	22.6	22.6	22.5	22.1	21.4	20.3	16.6	13.5	11.4	11.2	10.2	10.1
	SD	0.9	0.9	0.9	1.0	1.0	1.0	1.3	0.8	0.5	0.5	0.2	0.2
12:45	MEAN	22.9	22.9	22.9	22.4	21.7	20.7	16.9	13.7	11.4	11.2	10.2	10.0
	SD	0.9	0.9	0.9	0.9	1.0	0.9	1.3	0.8	0.4	0.4	0.1	0.1
13:00	MEAN	23.2	23.2	23.1	22.7	22.0	20.9	17.0	13.7	11.5	11.3	10.2	10.0
	SD	0.8	0.9	0.9	0.9	1.0	0.9	1.3	0.9	0.4	0.4	0.1	0.1
13:15	MEAN	23.4	23.5	23.4	22.9	22.3	21.1	17.1	13.6	11.5	11.3	10.2	10.0
	SD	0.9	0.9	0.9	0.9	0.9	0.9	1.6	0.7	0.4	0.3	0.1	0.1
13:30	MEAN	23.6	23.7	23.6	23.1	22.5	21.4	17.1	13.7	11.4	11.3	10.2	9.9
	SD	0.9	0.8	0.9	0.9	1.0	0.9	1.5	1.0	0.3	0.4	0.1	0.1
13:45	MEAN	23.8	23.8	23.8	23.3	22.8	21.6	17.2	13.7	11.4	11.2	10.1	9.9
	SD	0.9	0.9	0.9	0.9	1.0	0.9	1.7	1.1	0.4	0.4	0.1	0.1

Table 4. Percentage of fish in the three zones of the WCS aquarium over 8 experiments, by observation period

Observation Period	Conditions		Percentage of Fish in Zone								
			Top			Thermocline			Bottom		
	Temperature	Feeding	Mean	Median	SD	Mean	Median	SD	Mean	Median	SD
1	Isothermal	no Food	33.0	28.1	22.1	15.4	15.4	9.1	51.6	54.1	21.6
2	Isothermal	no Food	27.4	27.3	15.8	16.9	16.6	12.5	55.8	54.7	16.6
3	Isothermal	no Food	22.6	21.3	9.8	18.1	20.6	10.8	59.4	61.8	10.1
4	Isothermal	Food	62.0	71.9	29.1	6.6	6.7	5.7	31.5	25.2	25.3
5	Isothermal	no Food	19.6	4.9	30.2	10.4	8.3	9.5	70.0	75.2	29.7
6	Stratified	no Food	2.2	2.3	1.4	69.1	69.1	16.7	28.7	27.7	17.5
7	Stratified	no Food	4.3	1.7	5.5	66.6	69.6	7.9	29.1	27.9	10.0
8	Stratified	Food	29.8	34.0	8.4	31.4	33.8	5.1	38.8	37.6	5.9
9	Isothermal	no Food	44.6	47.1	26.9	15.8	13.4	9.8	39.6	28.5	23.9

Table 5. Results of statistical comparisons (t-tests) of the percentage of chum salmon in 3 vertical zones of the WCS aquarium under 6 experimental conditions (n = 8).

Condition	Observation Period	Time	Zone					
			Top		Thermocline		Bottom	
			%	Probability	%	Probability	%	Probability
Isothermal, Food Vs.	4	PM	62.0 ± 29.1	0.004*	6.6 ± 5.7	0.014**	31.5 ± 25.3	0.035**
Isothermal, no Food	2	PM	27.4 ± 15.8		16.9 ± 12.5		55.8 ± 16.6	
Stratified, no Food Vs.	7	AM	4.3 ± 5.5	0.009*	66.6 ± 7.9	<0.0001*	29.1 ± 10.0	0.028**
Isothermal, no Food	1	AM	33.0 ± 22.1		15.4 ± 9.1		51.6 ± 21.6	
Stratified, no Food Vs.	6	PM	2.2 ± 1.4	0.003*	69.1 ± 16.7	0.001*	28.7 ± 17.5	0.026**
Isothermal, no Food	2	PM	27.4 ± 15.8		16.9 ± 12.5		55.8 ± 16.6	
Stratified, Food Vs.	8	PM	29.8 ± 8.4	<0.0001	31.4 ± 5.1	0.001*	38.8 ± 5.9	0.153^{NS}
Stratified, no Food	6	PM	2.2 ± 1.4		69.1 ± 16.7		28.7 ± 17.5	
Stratified, Food Vs.	8	PM	29.8 ± 8.4	0.013**	31.4 ± 5.1	<0.0001*	38.8 ± 5.9	0.409^{NS}
Isothermal, Food	4	PM	62.0 ± 29.1		6.6 ± 5.7		31.5 ± 25.3	
Stratified, Food Vs.	8	PM	29.8 ± 8.4	0.649^{NS}	31.4 ± 5.1	0.018**	38.8 ± 5.9	0.013**
Isothermal, no Food	2	PM	27.4 ± 15.8		16.9 ± 12.5		55.8 ± 16.6	

^{NS} = not significant.

* = significant with family-wise error rate of 0.05.

** = significant with family-wise error rate of 0.10.

Table 6. Results of statistical comparisons (t-tests) of the swim speed (n = 147-167) of juvenile chum salmon under 6 experimental conditions (n = 8) in the WCS aquarium.

Experimental Condition	Observation Period	Time	Swimming Speed			
			$cm \cdot s^{-1}$	Probability	$BL \cdot s^{-1}$	Probability
Isothermal, Food Vs.	4	PM	9.4 ± 3.8	0.003*	1.1 ± 0.6	0.003*
Isothermal, no Food	2	PM	4.0 ± 3.0		0.5 ± 0.5	
Stratified, no Food Vs.	7	AM	3.7 ± 2.8	0.797^{NS}	0.5 ± 0.4	0.873^{NS}
Isothermal, no Food	1	AM	4.6 ± 3.6		0.6 ± 0.6	
Stratified, no Food Vs.	6	PM	4.0 ± 2.8	0.444^{NS}	0.5 ± 0.4	0.959^{NS}
Isothermal, no Food	2	PM	4.0 ± 3.0		0.5 ± 0.5	
Stratified, Food Vs.	8	PM	17.3 ± 5.9	<0.0001*	2.1 ± 0.9	<0.0001*
Stratified, no Food	6	PM	4.0 ± 2.8		0.5 ± 0.4	
Stratified, Food Vs.	8	PM	17.3 ± 5.9	<0.0001*	2.1 ± 0.9	<0.0001*
Isothermal, Food	4	PM	9.4 ± 3.8		1.1 ± 0.6	
Stratified, Food Vs.	8	PM	17.3 ± 5.9	<0.0001*	2.1 ± 0.9	<0.0001*
Isothermal, no Food	2	PM	4.0 ± 3.0		0.5 ± 0.5	

^{NS} = not significant.

* = significant with family-wise error rate of 0.05.

Table 7. Results of statistical comparisons (t-tests) of the time chum salmon spent in the top zone of the WCS aquarium under 5 experimental conditions (n = 8).

Experimental Condition	Observation Period	Time	Duration (s)	
			mean ± SD	Probability
Isothermal, Food Vs.	4	PM	>23 ± 23.8	0.641[NS]
Isothermal, no Food	2	PM	>23 ± 24.8	
Stratified, no Food Vs.	6	PM	3.2 ± 3.3	0.007*
Isothermal, no Food	2	PM	>23 ± 24.8	
Stratified, Food Vs.	8	PM	10.7 ± 8.0	0.010*
Stratified, no Food	6	PM	3.2 ± 3.3	
Stratified, Food Vs.	8	PM	10.7 ± 8.0	0.04**
Isothermal, Food	4	PM	>23 ± 23.8	
Stratified, Food Vs.	8	PM	10.7 ± 8.0	0.03**
Isothermal, no Food	2	PM	>23 ± 24.8	

[NS] = not significant.

* = significant with family-wise error rate of 0.05.

** = significant with family-wise error rate of 0.10.

Table 8. Distribution of chum salmon in relation to different thermal regimes (18, 25, 30°C), total gas pressure, and the presence of food, in the WCS aquarium (n = 1).

Conditions		% Fish in Zone			Temperature (°C)			TGP (%)		DO_2 (% sat.)		Salinity	Observation
		Top	Thm	Bot	Top	Mid	Bot	Top	Bot	Top	Bot	(‰)	Time (min)
Isothermal	MEAN	65	10	25	10.1	10.4	9.8	99.7	99.9	96.1	95.7	27.4	4
	SD	23	4	25									
Thermal stratification	MEAN	87	3	10	18.6	10.4	9.8	102.8	98.7	93.8	94.6	27.4	8
	SD	9	5	8									
Thermal stratification TGP	MEAN	66	14	20	18.6	10.7	10.0	113.5	100.8	93.4	93.6	27.4	8
	SD	7	6	4									
Thermal stratification TGP, Food	MEAN	83	2	14	18.0	10.8	9.9	113.1	101.5	92.2	93.1	27.4	4
	SD	6	3	5									
Thermal stratification TGP*, Food	MEAN	89	1	11	18.5	10.6	9.7	111.4	100.6	86.9	92.8	27.4	4
	SD	3	3	2									
Thermal stratification	MEAN	78	6	16	18.2	11.1	9.9	99.2	95.6	88.1	91.1	28.1	8
	SD	22	5	22									
Thermal stratification TGP, Food	MEAN	51	11	38	25.4	11.0	9.9	112.2	97.3	91.1	91.8	28.1	13
	SD	13	6	15									
Thermal stratification TGP	MEAN	0	21	78	30.4	11.6	9.9	110.6	98.7	87.1	91.4	28.1	4
	SD	1	7	7									
Thermal stratification TGP, Food	MEAN	32	11	57	30.4	11.6	9.9	109.0	98.4	85.5	91.3	28.1	6
	SD	22	5	22									

Top = Top zone, Thm = thermocline zone, Mid = middle zone, Bot = bottom zone, * = no air injection

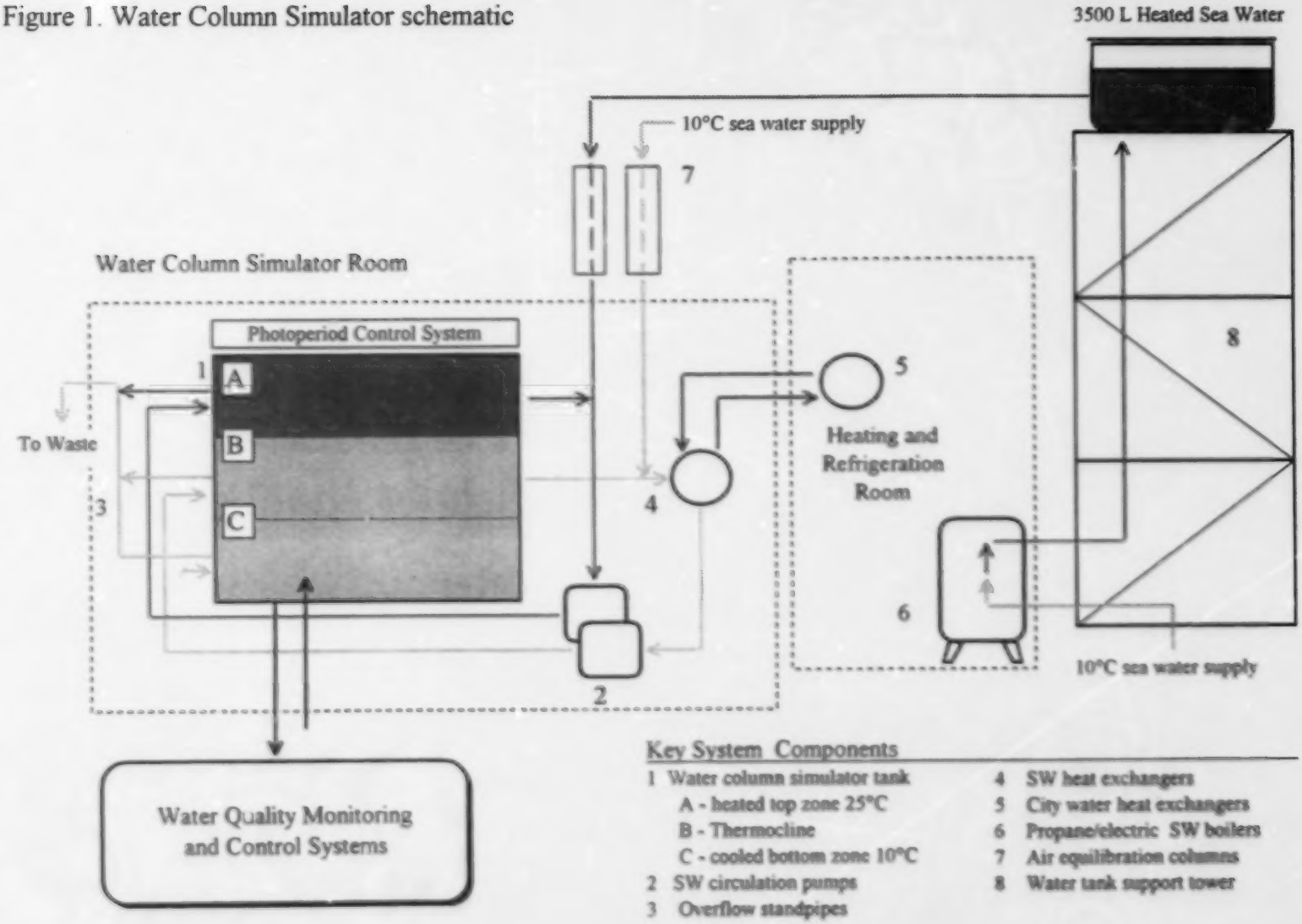
Table 9. The results of piece-wise, non-linear regression analysis applied to the percentage of fish in the top zone of the WCS aquarium over 7 experiments.

	Model Parameters					
Expt #	a1	k1	a4	k2	a5	Corrected R-Square
1	13.9	17.5	94.1	18.3	-20.7	0.849
2	17.2	14.9	90.7	16.9	-14.0	0.907
3	36.1	13.2	95.5	16.9	-16.1	0.895
4	21.8	14.2	96.6	18.5	-20.0	0.756
5	26.6	12.0	80.8	19.4	-18.7	0.820
6	31.8	13.3	90.8	17.5	-16.9	0.722
7	23.0	13.6	61.9	17.6	-9.6	0.547
Mean of 1 - 7	23.1	13.7	83.5	17.9	-14.7	0.684

Table 10. Robustness test results of the piece-wise non-linear model run with (n-1) weeks to determine if the estimates of k1 and k2 changed with data removal.

Week Removed	Model Parameters				
	k1	k2	a1	a4	a5
1	13.6	17.5	23.4	86.7	-14.2
2	13.5	18.0	25.1	83.1	-14.6
3	13.9	18.1	20.1	81.7	-14.8
4	13.5	17.8	23.6	80.9	-14.0
5	13.8	17.8	23.7	84.0	-14.9
6	13.8	18.0	21.1	82.6	-14.5
7	13.7	18.0	23.2	86.6	-16.0
	13.7	17.9	23.1	83.5	-14.7

Figure 1. Water Column Simulator schematic



Key System Components

1 Water column simulator tank
- A - heated top zone 25°C
- B - Thermocline
- C - cooled bottom zone 10°C

2 SW circulation pumps
3 Overflow standpipes
4 SW heat exchangers
5 City water heat exchangers
6 Propane/electric SW boilers
7 Air equilibration columns
8 Water tank support tower

Figure 2. Time mortality curves for juvenile chum salmon exposed to 25°C salt water (± elevated TGP).

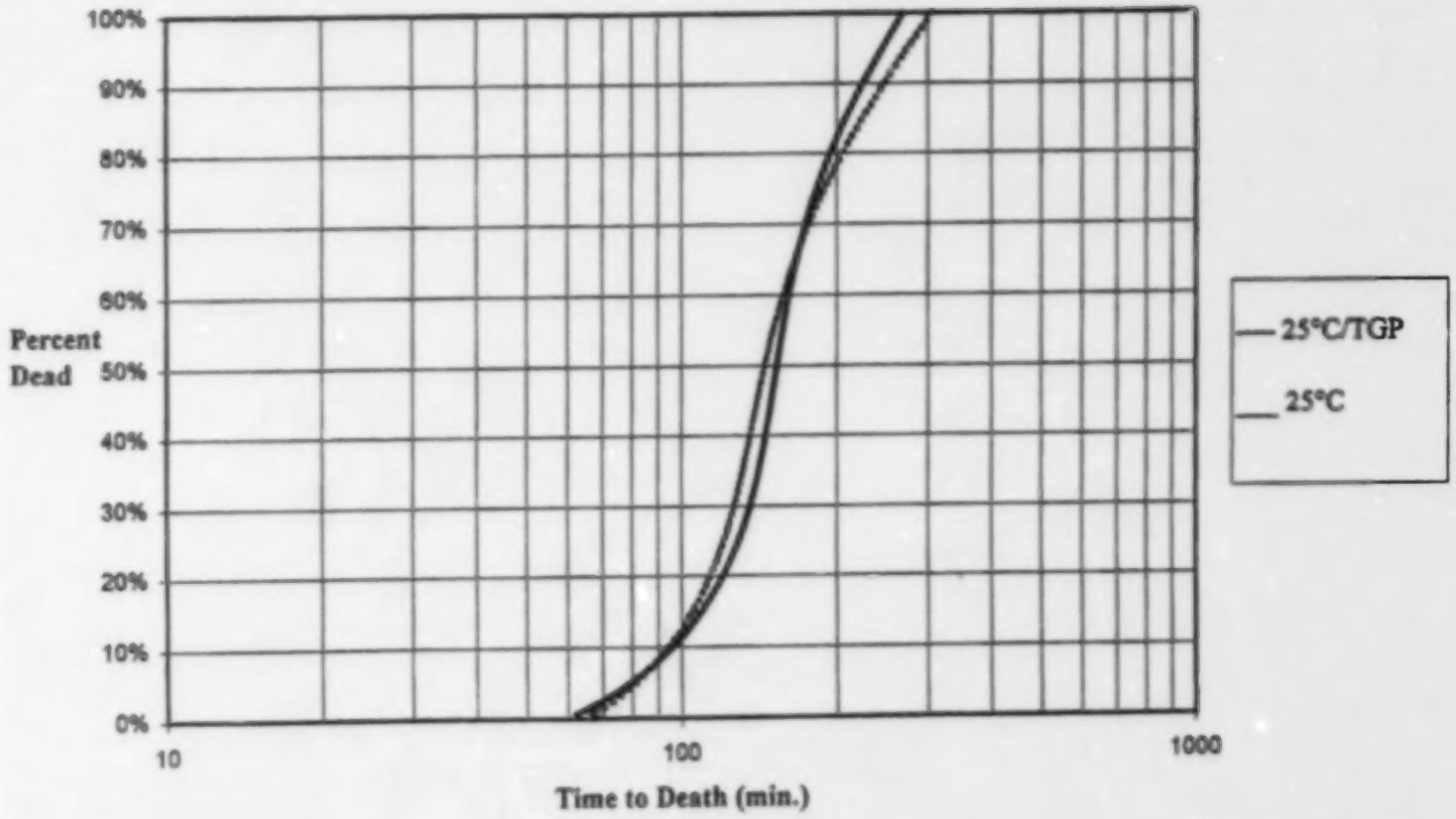


Figure 3. Temperature changes recorded by data loggers (#1-#12) at specific depths in the WCS aquarium during transition from isothermal to thermally stratified conditions.

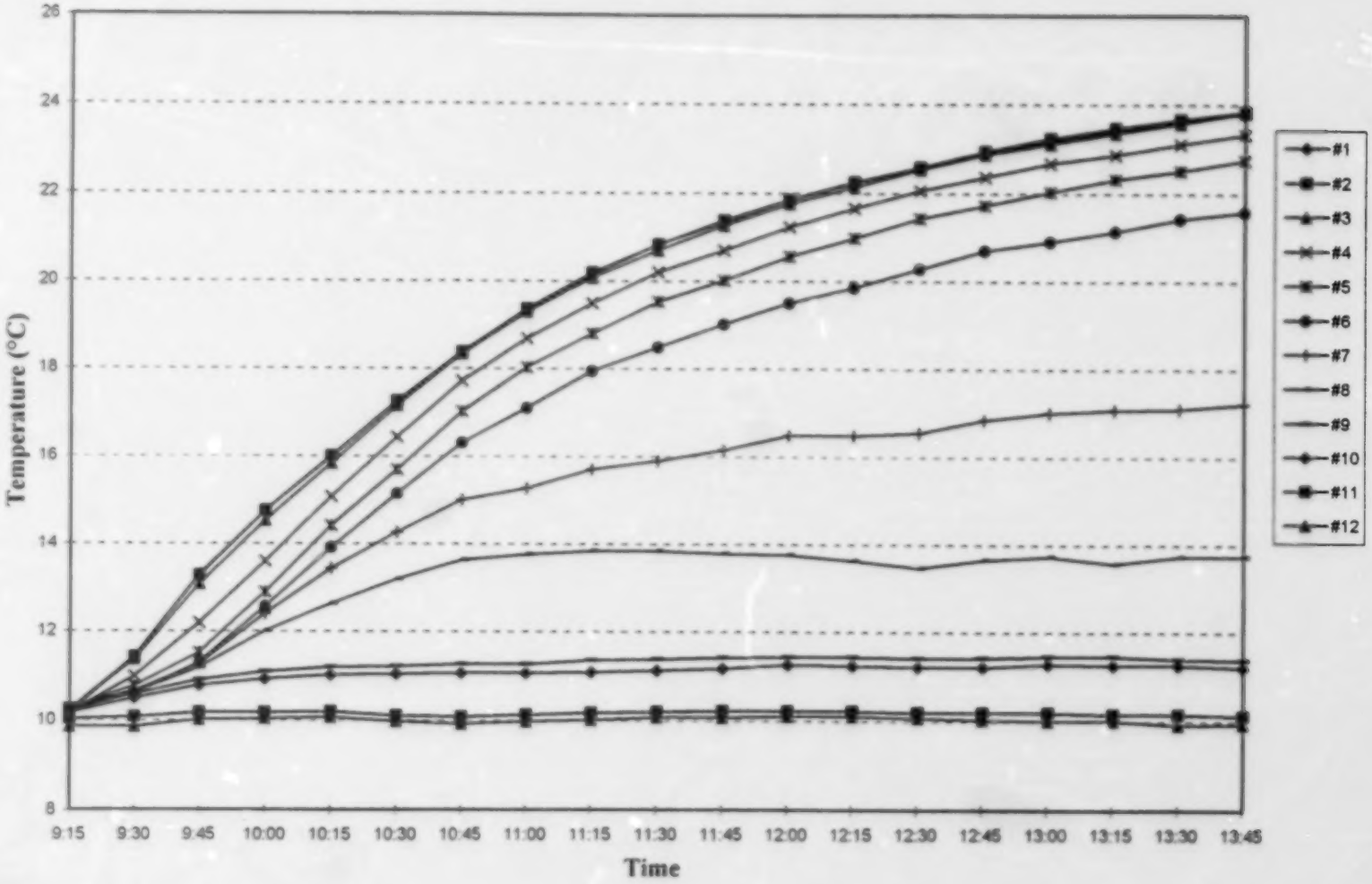


Figure 4. Precise location of individual chum salmon in the WCS aquarium (observation period 1 - isothermal AM)

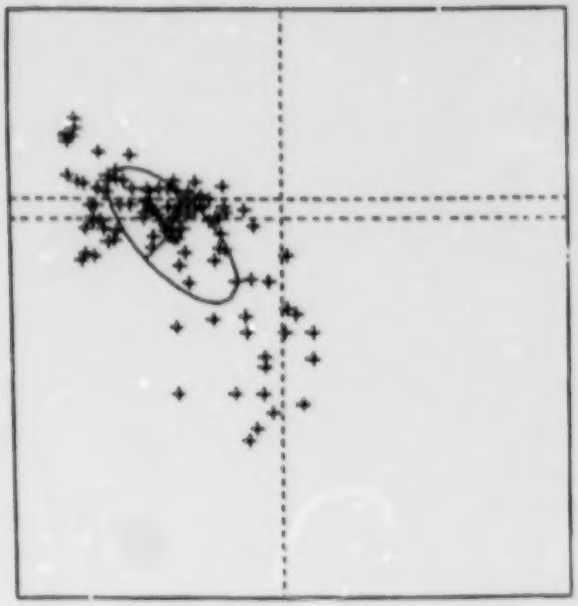


Figure 5. Precise location of individual chum salmon in the WCS aquarium (observation period 3 - isothermal AM)

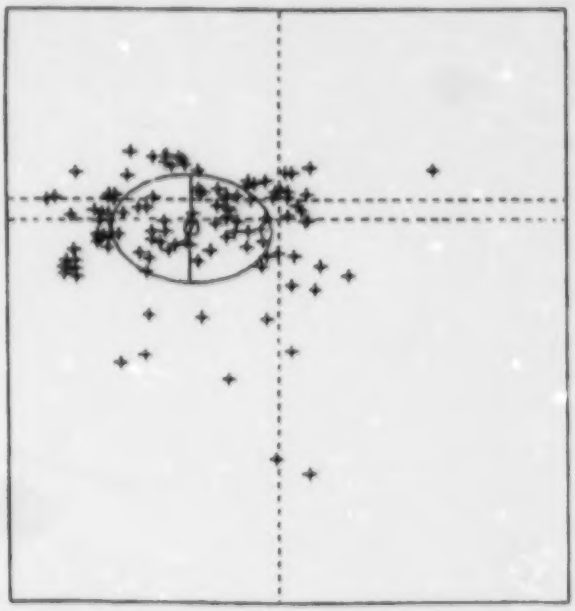


Figure 6. Precise location of individual chum salmon in the WCS aquarium (observation period 5 - isothermal AM)

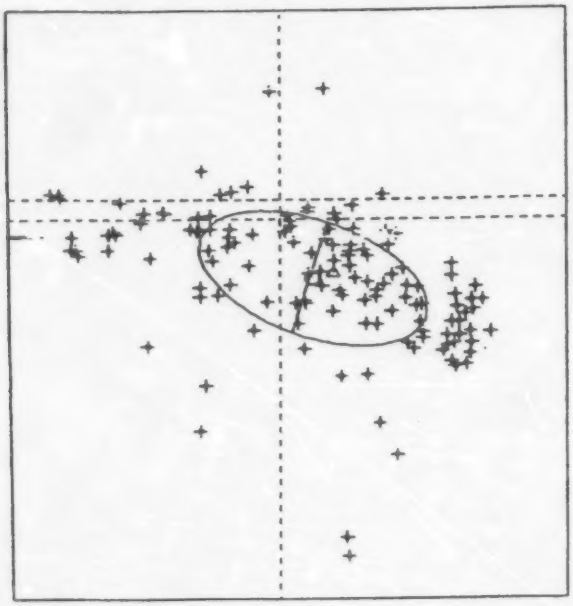


Figure 7. Precise location of individual chum salmon in the WCS aquarium (observation period 9 - isothermal AM)

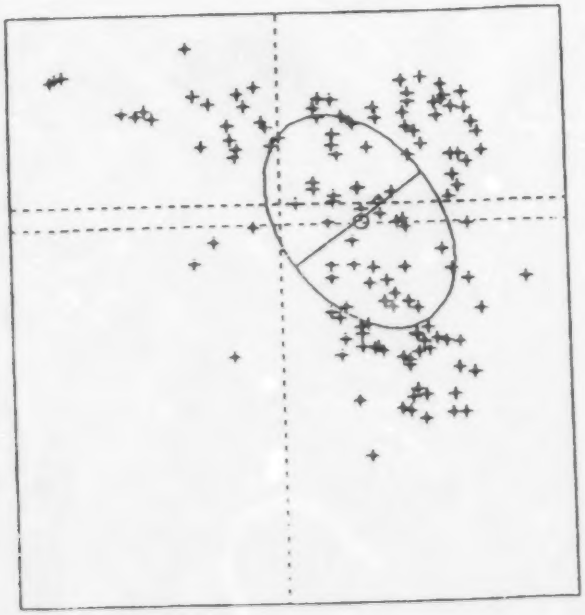


Figure 8. Precise location of individual chum salmon in the WCS aquarium (observation period 7 - thermally stratified AM)

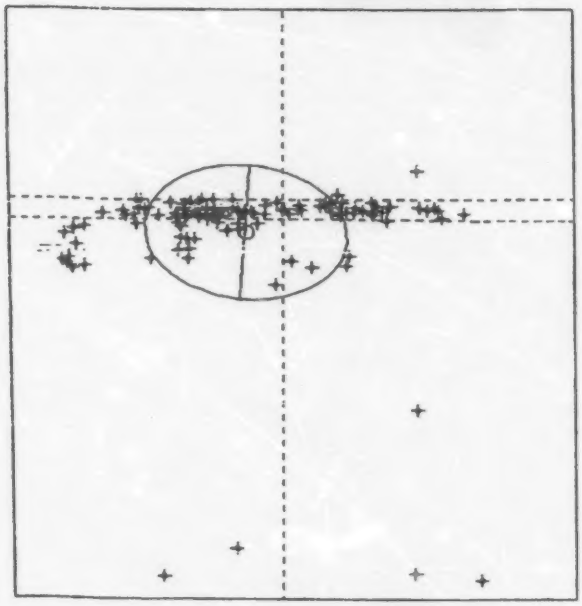


Figure 9. Precise location of individual chum salmon in the WCS aquarium (observation period 2 - isothermal PM)

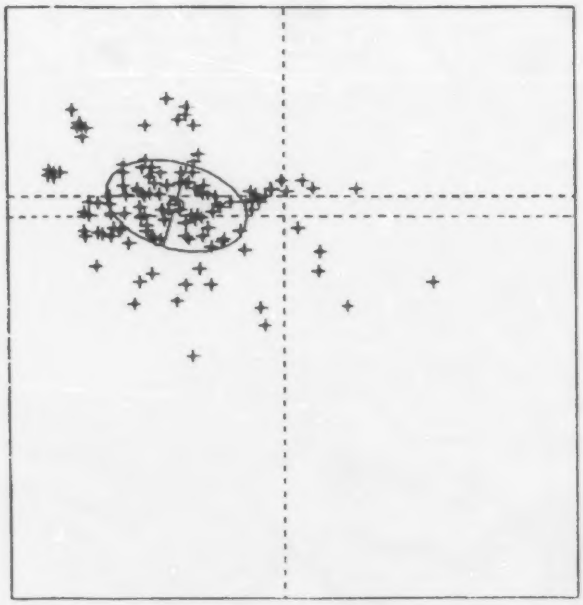


Figure 10. Precise location of individual chum salmon in the WCS aquarium (observation period 4 - isothermal, food PM)

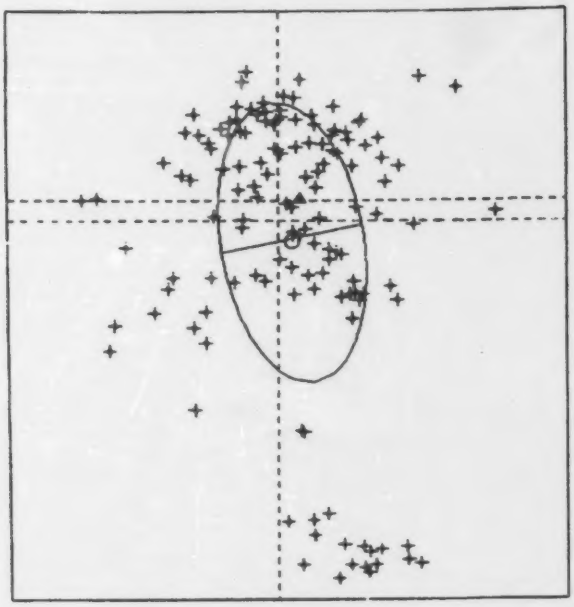


Figure 11. Precise location of individual chum salmon in the WCS aquarium (observation period 6 - thermally stratified PM)

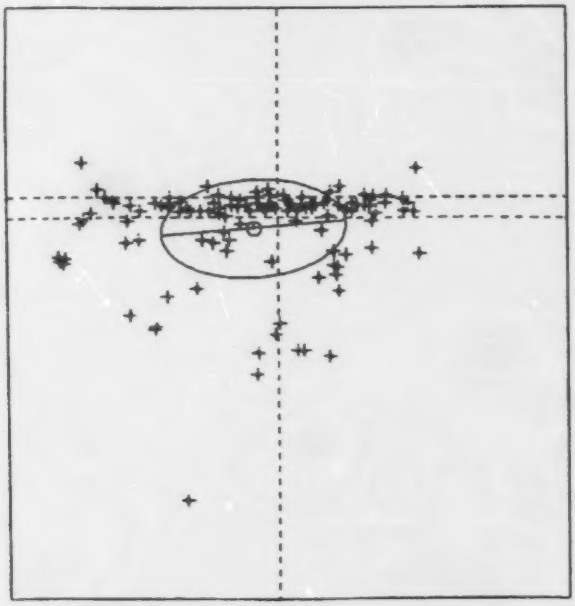


Figure 12. Precise location of individual chum salmon in the WCS aquarium (observation period 8 - thermally stratified, food PM)

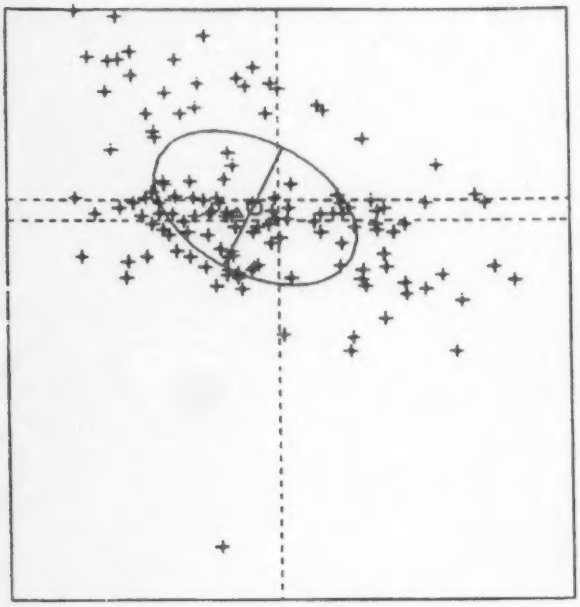


Figure 13. Response of juvenile chum salmon to temperature change in the surface waters of the WCS aquarium, estimated by piece-wise non-linear regression.

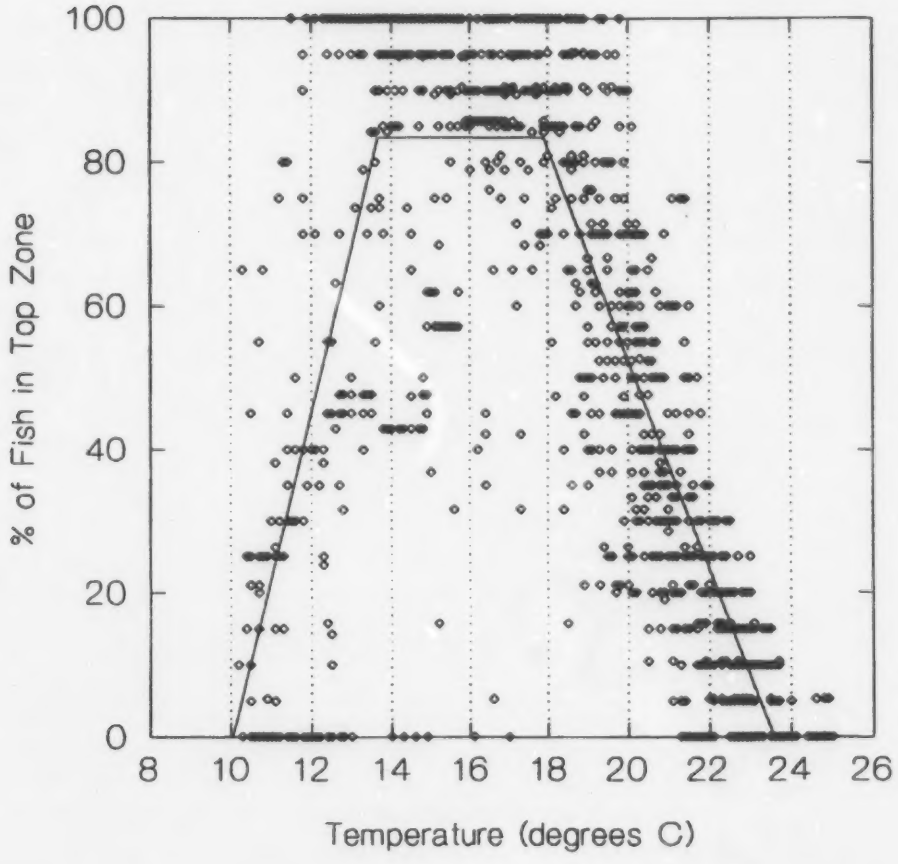


Figure 14. Presence of juvenile chum salmon in the thermocline during temperature change in the surface waters of the WCS aquarium, estimated by piece-wise non-linear regression.

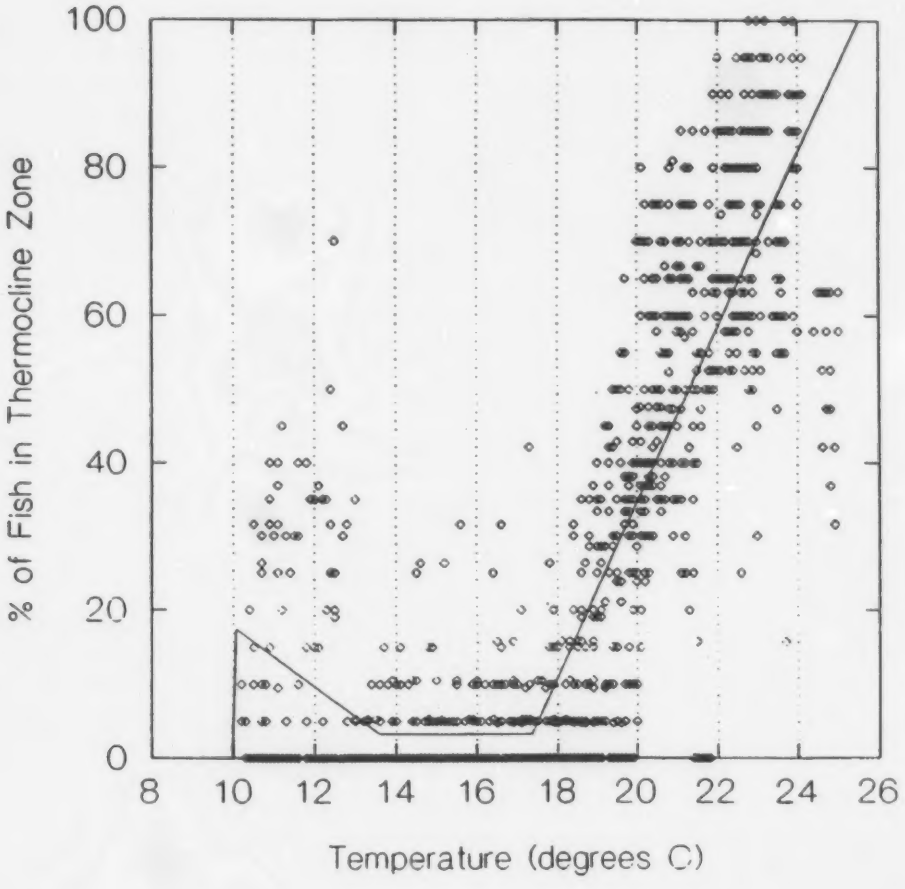


Figure 15. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 10.4 - 11.3°C)

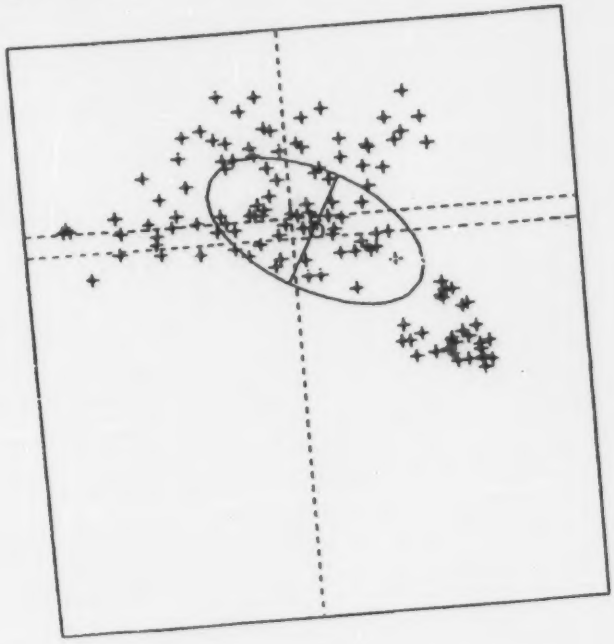


Figure 16. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 11.3 - 12.1°C)

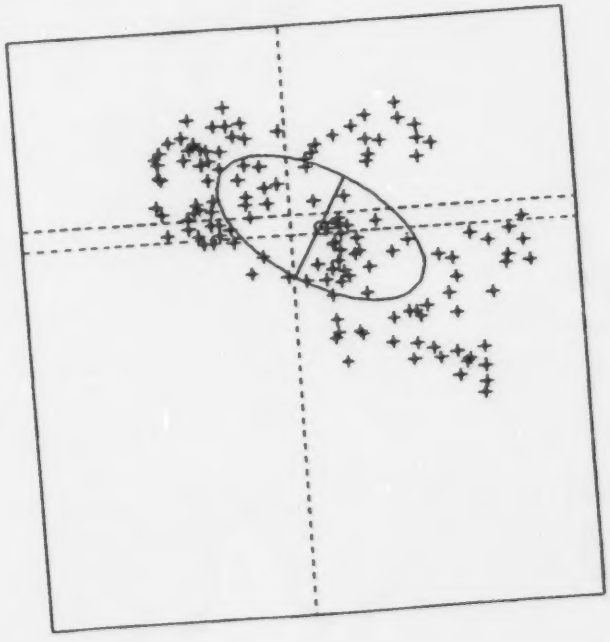


Figure 17. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 12.1 - 13.1°C)

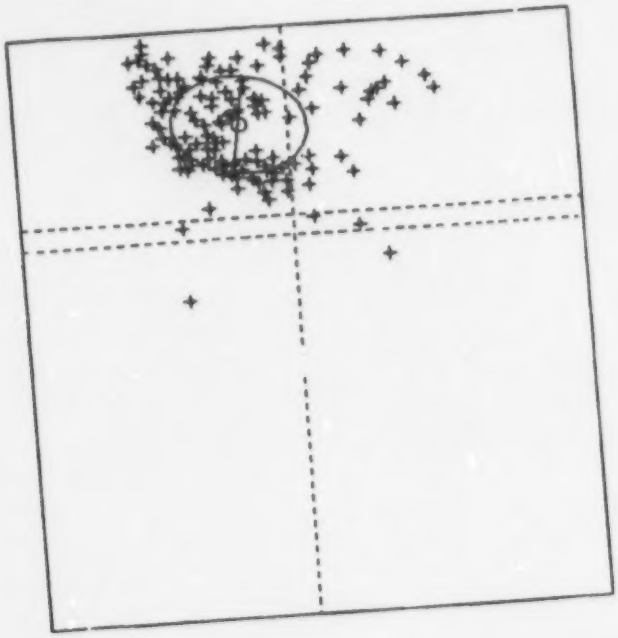


Figure 18. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 13.1 - 14.1°C)

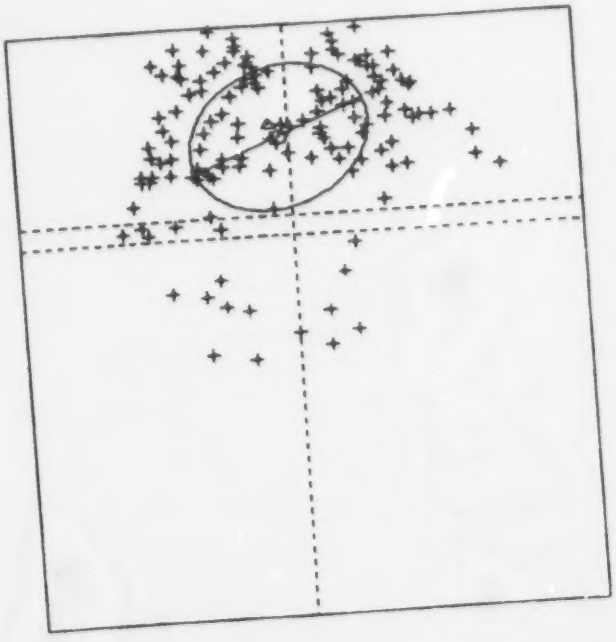


Figure 19. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 14.1 - 15.2°C)

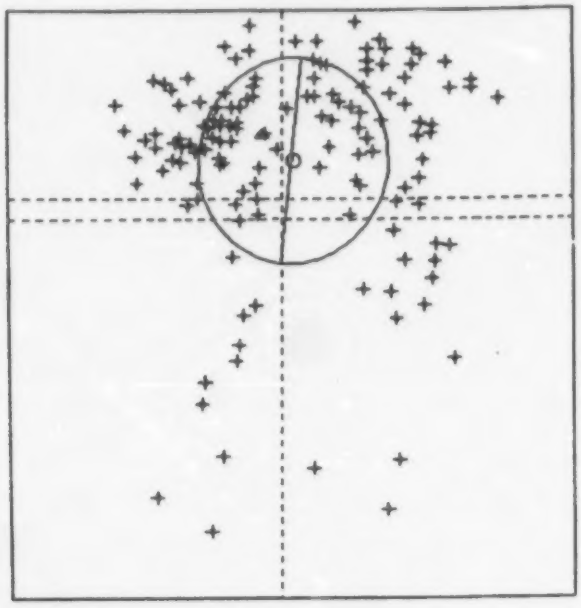


Figure 20. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 15.2 - 16.0°C)

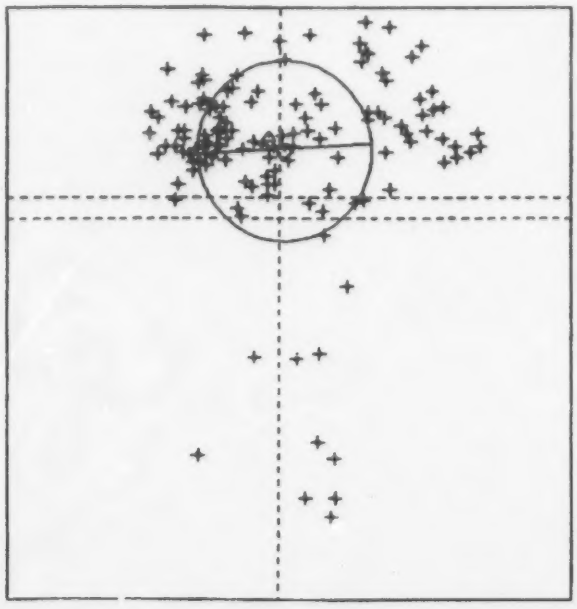


Figure 21. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 16.0 - 17.1°C)

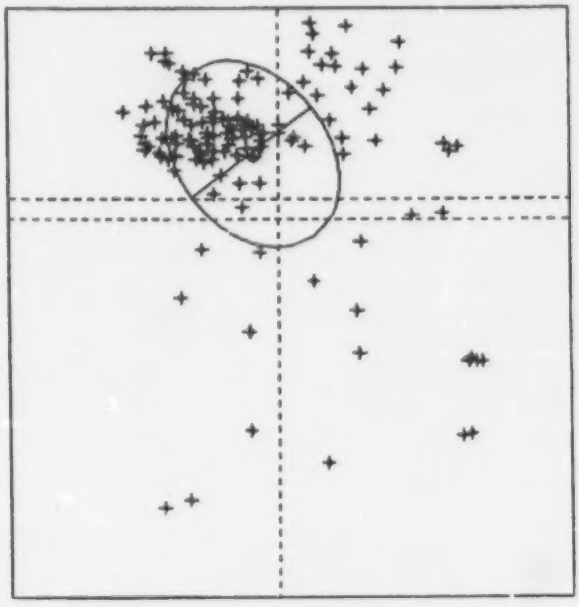


Figure 22. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 17.0 - 18.0°C)

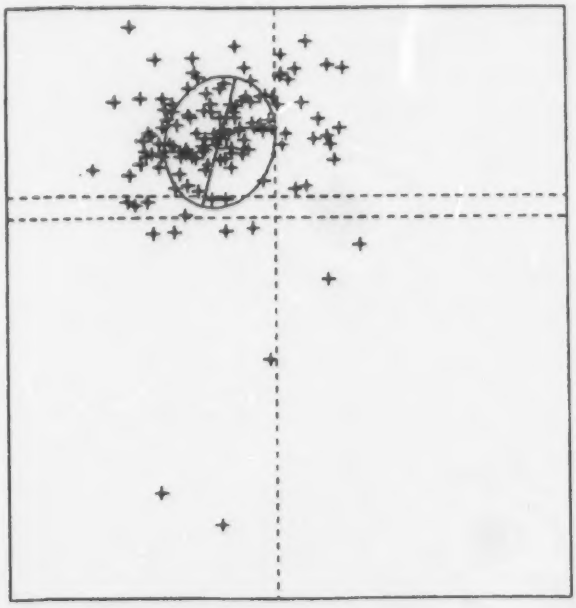


Figure 23. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 18.0 - 19.0°C)

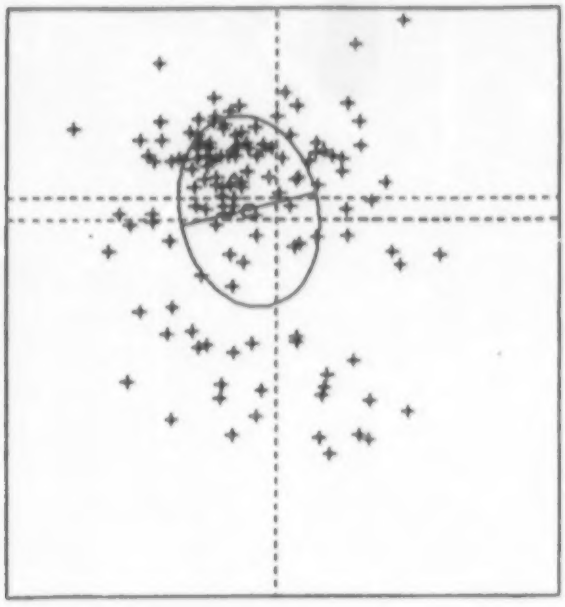


Figure 24. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 19.0 - 20.0°C)

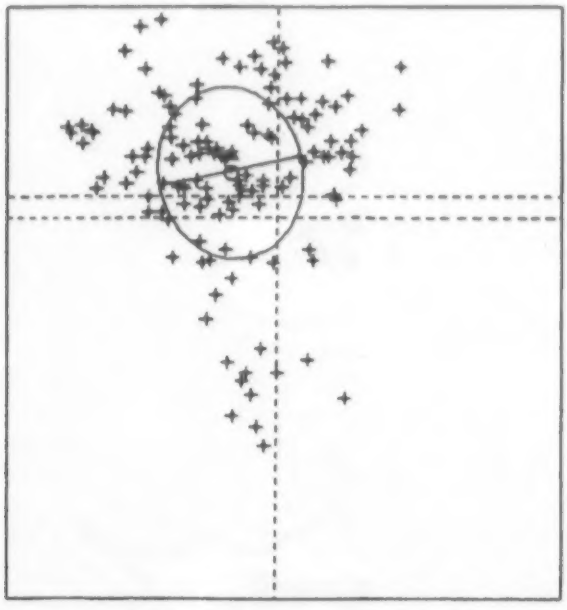


Figure 25. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 20.0 - 21.1°C)

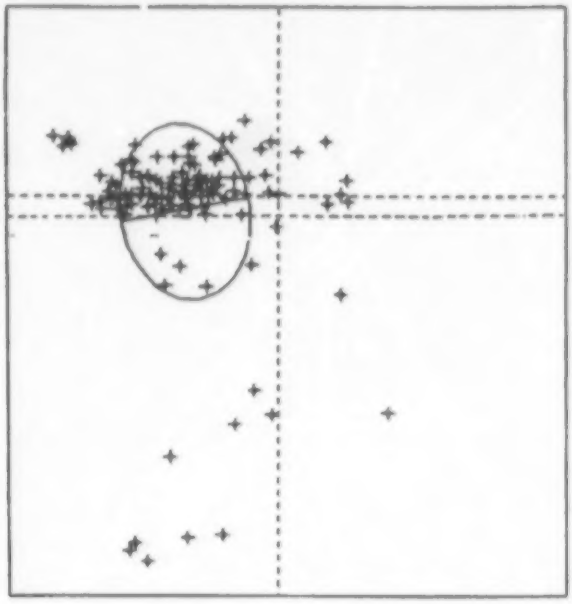


Figure 26. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 21.1 - 22.0°C)

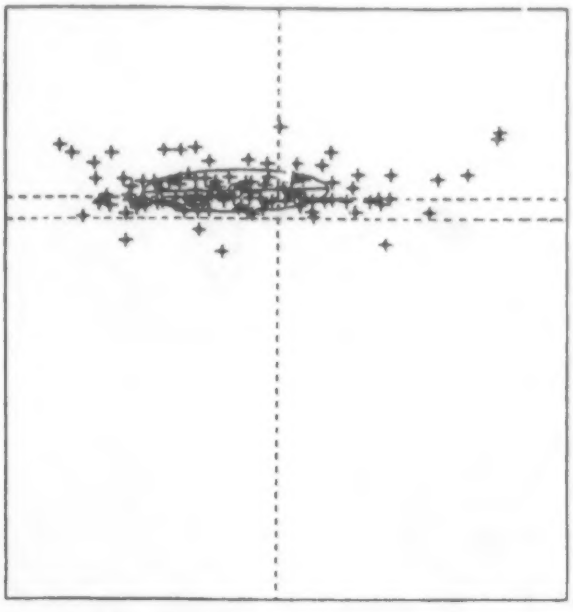


Figure 27. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 22.0 - 23.0°C)

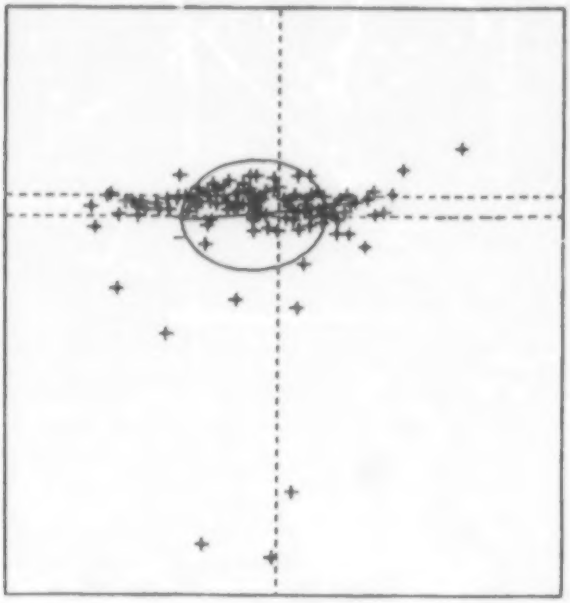


Figure 28. Precise location of individual chum salmon in the WCS aquarium (top zone temperature 23.0 - 23.7°C)